A GEOSPATIAL DATA INTEGRATION FRAMEWORK FOR MAPPING AND MONITORING TROPICAL LANDSCAPE DIVERSITY IN COSTA RICA'S SAN JUAN – LA SELVA BIOLOGICAL CORRIDOR

A Dissertation

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by

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AUTHORIZATION TO SUBMIT DISSERTATION

This dissertation of Steven E. Sesnie submitted for the degree of Doctor of Philosophy with a major in Natural Resources and titled “A geospatial data integration framework for mapping and monitoring tropical landscape diversity in Costa Rica’s San Juan – La Selva Biological Corridor”, has been reviewed in final form. Permission, as indicated by the signatures and dates given below, is now granted to submit final copies to the College of Graduate Studies at the University of Idaho (UI), and to the Postgraduate School at Centro Agronómico Tropical de Investigatión y Enseñaza (CATIE) for approval.

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ABSTRACT

Landcover change has substantially reduced the amount of tropical rain forest since the 1950s. Little is known about the extent of remaining forest types. A multivariate analysis of 144 forest plots across Costa Rica's San Juan – La Selva Biological Corridor resulted in eight floristically defined old-growth forest categories. Spectral separability was tested between categories using Landsat TM bands and vegetation indices for old-growth types, palm swamps, tree plantations and regrowth. Image filtering and NDVI increased spectral separability among categories by 30%. Separability tests resulted in seven well-discriminated forest categories.

Factors driving forest beta-diversity are not well quantified for wet tropical environments. We examined the relationship between rain forest composition and environmental variation for a 3000 km^2 area in northeastern Costa Rica. Mid- to upper-canopy tree species abundance and soil characteristics were measured from 127, 0.25-ha plots across Caribbean lowlands and foothills. Partial Mantel tests produced significant correlations between floristic distance and soil, terrain, and climate variables controlling the effects of geographical distance. Niche-factors showed a significant trend with forest composition more than dispersal limitation or disturbance related factors.

Variables such as terrain features, climatic variation and Landsat TM bands associated with forest composition were assessed with two decision tree models. Thirty-two landcover types were compared for a 15-year time interval. Ten were floristic alliances from a cluster analysis of forest plots and wetland categories. A subset of 12 spectral and spatial predictor variables produced accuracies of 93%±7% and 83%±15% for *QUEST* and *CRUISE* classifiers, respectively. The *QUEST* classifier was accurate for habitat mapping and change detection important to biodiversity monitoring objectives.

A 1996 Forestry Law initiated environmental service payments and prohibited forest conversion. Landcover changes were compared before and after 1996 and linked to landowner surveys. Carbon services from secondary forests were examined above- and belowground. Natural forest loss declined from -1.43 to -0.20% yr^{-1}. Secondary forest carbon storage approached primary forest levels after 25-30 years, though few landowners retained tree regeneration. The Costa Rican experience provides evidence that payments were effective in retaining natural forest and recruiting tree cover mainly via tree plantations.

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Wayde Morse, Jessica Schedlbauer and I designed an integrated project to compare large area forest cover change and its relationship to land use policy, human behavior and ecosystem processes important to Costa Rica's conservation objectives. Their dedication to successfully complete this research amid numerous challenges is worthy of special praise. Bryan Finegan provided important guidance and mentorship for integrated aspects of this project in addition to important editorial remarks on early versions of Chapter 4. I would especially like to thank Celia Harvey and J.D. Wulfhorst for providing many useful comments on drafts of the team written Chapter 4.

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DEDICATION

To Stacy and Ashley, for their unwavering patience

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INTRODUCTION

Validated methods to discriminate diverse tropical vegetation types with remotely sensed data have become progressively important following the International Convention on Biological Diversity (CBD) (UNEP 1992, Nagendra and Gadgil 1999). Accelerated deforestation since the 1950s has left scattered old-growth forest remnants and tree regrowth amid agricultural lands over much of Central and South America (Houghton 1994, Mayaux et al. 2005). Reducing rates of habitat loss prior to the year 2010 is a principal objective established by CBD. The 1992 United Nations Framework Convention on Climate Change targets aforestation and reforestation areas as carbon sinks that can potentially restore a level of forest connectivity and wildlife habitat within fragmented landscapes (Lamb et al. 2005). National conservation strategies towards these ends are linked to environmental services such as watershed and biodiversity protection, climate stabilization and forest resources important to humans (Millennium Ecosystem Assessment 2005).

Creating suitable landcover information for natural resource planning and prioritizing conservation activities will require methods to integrate data from a variety of earth observation systems (Kerr and Ostrovsky 2003). Acceptable approaches must ultimately be ecologically valid and operationally feasible (Defries and Townsend 1999, Brown de Colstoun et al. 2003).

Limited knowledge about the distribution and extent of tropical rain forest types inhibit conservation activities aimed at maintaining regional floristic diversity (Chust et al. 2006). The objective of Chapter 1 is to examine species and spectral differences for Costa Rican rain forest composition measured along environmental gradients. Floristically defined old-growth forest types are needed for tropical rain forest where most of the world's biodiversity is centered (Salovaara et al. 2004). Vegetation studies from Amazonian rain forest suggest that a lack of field data, as much as the spectral and spatial grain of satellite sensors, has limited distinguishing among forest types (Tuomisto et al. 1995, Tuomisto et al. 1998). Mid- to upper-canopy tree, palm, and fern species were expected to show composition differences at broad spatial scales (Lieberman et al. 1996, Pyke et al. 2001) that are potentially related to reflectance values from Landsat TM bands (Tuomisto et al. 2003a). Prior investigations using Landsat TM and ETM+ data confirm accurate discrimination among rain forest from mainly contrasting structural conditions such as palm swamps and bamboo forest (Foody and Hill 1996, Lobo and Guillison 1998, Pedroni 2003) or distinctive vegetation on poor fertility soils (Tuomisto et al. 1995). Tree species differences across the Panama Canal Watershed have shown a significant correlation with Landsat TM bands (Chust et al. 2006), though from dry season images and plots spanning a deciduous gradient (Condit et al. 2000). Less is known about the spectral separability among Caribbean rain forest types with little apparent seasonal variation (e.g., deciduousness) or structural differences.

Factors driving forest beta-diversity defined as turnover in tree species composition (Condit et al. 2002) are not well quantified for wet tropical environments given many logistical constraints (Ruokolainen et al. 1997). Chapter 2 compares floristic composition measured from forest plots with variation in environmental and geographical distance at a landscape-scale. Current studies of tropical rain forest composition argue environmental determinism versus seed dispersal limitation or random disturbance factors as principal mechanisms underlying floristic variation (Hubbell 2001, Tuomisto et al. 2003b, Jones et al. 2006, Chust et al. 2006). Geographical distance can be an important factor related to forest composition that accounts for unmeasured variables or barriers to seed dispersal (Chust et al. 2006). Lacking from Central American studies are soil chemical and physical data matched with measurements of forest composition at a landscape-scale (Condit et al. 2002, Chust et al. 2006). Soil, terrain and climatic characteristics determined for each forest plot are used for comparison with distance matrices derived from floristic composition. To test alternative hypotheses, environmental and geographical distances are compared with floristic distance via Partial Mantel correlations to while controlling the affect of a third related factor (*see* Legendre and Fortin 1989, Poulsen et al. 2006).

Chapter 3 builds on results from chapters 1 and 2 by evaluating two decision tree (DT) classifiers for integrated mapping and monitoring of tropical rain forest and disturbance related landcover categories (e.g., forest regrowth, tree plantations and agricultural land use). DT classifiers are relatively unexplored for mapping of tropical forest types (*but see* Muchoney et al. 2000). Classical "niche theory" and gradient analysis are central to DT applications for predictive vegetation modeling and pattern recognition (Franklin 1995). Landsat TM bands combined with biophysical factors compared in chapters 1 and 2 were expected to compensate for low spectral separation among some landcover categories. Non-parametric DTs have been shown to be more capable than other methods for integrating data to solve complex ecological classification problems (De'ath and Fabricius 2000).

Environmental monitoring via remotely sensed data has traditionally meant estimating broadly defined "forest cover" and deforestation rates for Costa Rica (Kleinn et al. 2002). Deforestation estimates have played a fundamental role in adjusting forest policies, though often with uncertainty regarding the successional or structural status of forests (De Camino et al. 2000). Present environmental programs and policy reforms in Costa Rica seek to retain and recover private forests for watershed and biodiversity protection, carbon sequestration and aesthetic values (Chomitz et al. 1999). Monitoring procedures and application of remote sensing instruments require discriminating forest structural types, to the greatest extent possible, with differing carbon and habitat values (Castro et al. 2003).

Enhanced landcover classifications investigated in Chapter 3 were part of a larger integrated project. Chapter 4 was a case study to examine forest changes related to recent environmental policy reforms. Costa Rica's 1996 Forest Law (no. 7575) established a national definition of forest, instituted policy that prohibits forest conversion to any other land use and created an payment program (*pago por servicios ambientales*, PSA) to compensate landowners for environmental services (Snider at al. 2003). Forest and landscape changes before and after 1996 are linked to landowner decisions that influence ecosystem processes such as forest carbon cycling important to national and international environmental objectives. Contracts for reforestation, forest management and protection between the Costa Rican government and private landowners have expended US$124 million on PSA for >5,000 km^2 of land (FONAFIFO 2006). Because of excess demand for participation in the program, payments are targeted in areas such as Costa Rica's portion of the Mesoamerican Biological Corridor (Chomitz et al. 1999, García 1996). Payments are aimed at landowners with small to medium-sized landholdings. PSA is voluntary, thus objectives to retain and recover forest on a large scale are dependent on participation and perceived benefits. Few studies have determined whether PSA successfully contributes to natural forest retention and recruitment in locations where programs have been implemented.

The study area for this research was confined to an 8,000 km^2 landscape including the 2,425 km^2 San Juan – La Selva (SJ-LS) Biological Corridor between protected areas in northern Costa Rica and Nicaragua. The corridor initiative seeks to retain private forests as linkages between protected areas in addition to vegetation types representative of the region's floristic diversity (Chassot and Monge 2002). The area has been a primary focus of PSA since 1996 (Snider et al. 2003). Land use histories outside of protected areas in this region are characterized by a rapid colonization period with high forest conversion to cattle pastures from the 1960s to the late 1980s followed by a post-settlement period of intensified agricultural use (Butterfield 1994). Remnant forest and swamplands consist of small fragments of a few hectares in size to large contiguous forest patches >1000 ha along the boarder with Nicaragua. Natural forests are interspersed with pasture systems, perennial and seasonal crops, tree plantations and small patches of secondary forest re-growth in addition to riparian forest remnants (i.e., narrow forest corridors retained along rivers and streams) (Read et al. 2001).

The study area is part of the Isthmian-Atlantic moist forest ecoregion that extends from the southeastern Caribbean side of Nicaragua to Panama's northern coast (Olson et al. 2001). The biophysical environment and vegetation are strongly influenced by elevation that ranges from sea level to >3000m over the landscape (Lieberman et al. 1985, Lieberman et al. 1996). The lowlands are a mixture of steep hilly terrain, alluvial terraces, and flat swamplands interrupted by low hills reaching 400m elevation. Monthly temperature averages near 24°C in the lowlands, but temperatures decrease to as low as 10°C at the highest elevations in the Central Mountains (Lieberman et al. 1996). Annual precipitation ranges from 4000mm in the central portion of the study area (Hartshorn and Peralta 1988, Grieve et al. 1990) to <2500mm in the western lowlands according to precipitation data by Hijmans et al. (2005). Much of the eastern lowlands and the foothills have consistently high rainfall throughout the year. Seasonally lower precipitation occurs in the western lowlands and Pacific slope of the Central Mountains with average monthly rainfall ≤100mm for 1-3 months.

The four chapters of this dissertation are formatted as manuscripts to be submitted for publication. Chapter 1 includes Dr. Bryan Finegan, Dr. Paul Gessler, Sirpa Thessler, Zayra Ramos, and Dr. Alistair Smith as co-authors and will be submitted the Journal of Applied Ecology. Chapter 2 includes Dr. Bryan Finegan, Dr. Paul Gessler and Zayra Ramos as co-authors that will be submitted to the journal Biotropica. Chapter 3 includes Dr. Paul Gessler, Dr. Bryan Finegan and Sirpa Thessler as co-authors and has been submitted to the journal

Remote Sensing of Environment for a special issue on Earth observation for biodiversity and ecology. Chapter 4 was co-authored by two other doctoral students, Jessica Schedlbuaer and Wayde Morse, along with Dr. Bryan Finegan, Dr. Celia A. Harvey, Dr. Steven Hollenhorst, Dr. Kathleen Kavanagh, Dr. Dietmar Stoian and Dr. J.D. Wulfhorst that was submitted to the journal Ecosystems. This jointly written chapter will also be included in the dissertations of Jessica Schedlbauer and Wayde Morse. The joint chapter is one of the outcomes of a project at the University of Idaho funded by the National Science Foundation Integrative Graduate Education and Research Traineeship (IGERT) program. As part of this project, we worked as a student team to develop and complete an interdisciplinary research project. The theme of this IGERT project, biodiversity conservation and sustainable production in tropical and temperate fragmented landscapes, provided the context for all of this dissertation research. Funding for my dissertation work came from an NSF-IGERT fellowship and a scholarship from the Organization of American States.

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Chapter 1

The multispectral separability of tropical rain forest types using Landsat TM imagery: a preliminary assessment in Costa Rica's San Juan – La Selva Biological Corridor

Summary

1. Estimating the extent of remaining tropical rain forest types is often limited by lack of information about tree species composition across broad geographic regions, though relevant to retaining complementary areas of high floristic diversity. Forest data integrated with multispectral information from satellite sensors have potential to fill information voids, but depend upon the degree of spectral separability at the resolution of data available satellite sensors.

2. Landsat Thematic Mapper (TM) data is often used source of spectral information available for rain forest areas. We compared Sorensen (Bray-Curtis) similarity values between rain forest types determined from a wide distribution of forest plots with spectral features from a Landsat TM image. Forest measurements were taken from mid- and upper-canopy trees, arborescent palms and ferns to compare differences in composition that potentially affect radiance values. Plots were located in forest remnants in a 3,000 km^2 portion of the Mesoamerican Biological Corridor in northern Costa Rica. Eight primary forest categories were derived using hierarchical cluster analysis and Non-Metric Multidimensional Scaling with canopy tree abundance data from 144, 0·25 and 1·0 hectare plots located along precipitation and elevation gradients. Georeferenced locations from palm swamps, forest re-growth and tree plantations were also acquired to make a total of 11 forest types used for paired spectral separability comparisons.

3. To enhance spectral sensitivity for differing forest composition and structural types, vegetation indices and textural occurrence filtering were compared. Our results show that enhancements such as textural filtering and the Normalized Difference Vegetation Index (NDVI) increased the number of well separated forest categories by as much as 30%. Comparisons among forest types using species and spectral separability tests resulted in 7 significantly different and well-discriminated forest categories. Combining the most poorly separated categories based on group members identified via cluster analysis increased the level of accuracy of a supervised image classification from 63% to 81%.

1. Statistical comparisons and classifications revealed that forest types with low compositional similarity were spectrally distinct from one another. These results are promising and suggest that broad-scale field sampling of rain forest vegetation along environmental gradients combined with remotely sensed data can produce ecologically meaningful habitat classifications. Further integration of climate and elevation data will likely improve classifications of floristic types.

Key-words: separability tests, Landsat TM imagery, tropical forest types, biodiversity, image enhancement, vegetation indices

Introduction

An emerging topic in tropical ecology examines differences in vegetation composition, often measured along environmental or geographical gradients, and spectral reflectance patterns observed from satellite sensors (Tuomisto *et al*. 1995; Tuomisto 1998; Tuomisto *et al*. 2003a, b; Chust *et al*. 2006). Floristic dissimilarity among rain forest habitats (i.e., beta diversity) is poorly defined for much of the humid tropics though relevant to planning for the conservation of complementary areas of high plant diversity (Tuomisto *et al*. 1995; Condit 1996; Ferrier 2002; Chust *et al*. 2006). Forest conversion to other land uses threatens to drastically reduce the number of tropical vegetation types with limited means to prioritize and focus conservation activities (Defries *et al*. 2005; Mayaux *et al*. 2005). Combining remotely sensed information with field data on forest composition and other ecological factors is an increasingly acknowledged approach to fill information voids (Tuomisto 1998; Kerr & Ostrovsky 2003). Significant progress has been made to determine and map floristically defined forest types for temperate biodiversity assessments with the aid of remotely sensed data (Scott & Jennings 1998; Jennings 2000; Turner *et al*. 2003). However, a number of challenges must be overcome prior to advancing floristic characterizations for tropical rain forest from both technical and theoretical points of view (Condit 1996).

One such challenge is estimating the extent to which local floristic detail for rain forests can be determined at the resolution (e.g., spatial and spectral grain) of available optical remote sensing systems (Kerr & Ostovsky 2003). Neotropical forests are typically characterized by physiognomic distinctiveness and macroclimatic conditions (Beard 1944; Holdridge 1967; UNESCO 1973) at map scales courser than the floristic variation observed among rain forest plots (Tuomisto *et al*. 1995). Amazonian and Central American studies reveal that terrain and soil characteristics influence floristic composition presumably at patch scales from a few hundreds of meters to many square kilometers in size (Tuomisto *et al*. 1995; Clark *et al*. 1999; Tuomisto *et al*. 2003a; Phillips *et al*. 2003). Clark *et al*. (1995) and Clark *et al*. (1999) found that local topography affect the spatial distribution of many rain forest trees and palm species. Common canopy trees, often used for temperate zone forest classification and tall palms may also show wide geographic distributions with general habitat requirements (Pitman *et al*. 2001; Ruokolainen & Vormisto, 2000; Vormisto *et al*. 2004). Disturbance, dispersal limitations and other historical events may also affect existing rain forest composition at a variety of spatial scales (Hubbell *et al*. 1999; Condit *et al*. 2000a; Condit *et al*. 2002; Chust *et al*. 2006). The weight of environmental factors relative to dispersal limitations and stochastic events is difficult to quantify and often a source of debate (Duivenvoorden *et al*. 2002; Ruokolainen & Tuomisto 2002). Moreover, the segment of the floristic community measured and geographic extent or location of the areas sampled can produce differing conclusions (Tuomisto *et al*. 2003a, b; Condit *et al*. 2002; Phillips *et al*. 2003; Vormisto *et al*. 2004). These constraints can pose practical limits for making predictions beyond sampled locations from available data sets (Condit 1996; Tuomisto e*t al*. 2003b).

Alternatively, multispectral images from the Landsat program's long-term archives cover most of the world's humid tropical forests and are easy to obtain relative to other environmental data (Tuomisto 1998). Spectral bands provide a means of measuring variation that has been linked to differences in tropical rain forest composition and site conditions (Tuomisto *et al*. 1995; Tuomisto *et al*. 1998). Investigations at broad spatial scales confirm accurate discrimination among rain forest types though often for contrasting structural conditions such as comparatively monospecific palm swamps, bamboo forests and savannas (Hill & Foody 1994; Foody & Hill 1997; Lobo & Guillison 1998; Nagendra & Gadgil 1999; Pedroni 2003; Tottrup 2004) or distinctive vegetation on poor fertility soils (Tuomisto *et al*. 1995).

Amazonian studies have recently demonstrated that previously unrecognized rain forest types show visual and statistical relationships between field data and Landsat Thematic Mapper (TM) and Enhanced Thematic Mapper (ETM+) spectral bands (Tuomisto *et al.* 1995; Tuomisto *et al*. 2003a, b; Rajaniemi *et al*. 2005; Salovarra *et al*. 2005). Tuomisto *et al*. (2003b) report that vegetation associations of indicator plants measured over topographic gradients were well correlated with soil factors and TM bands, primarily for the near- (NIR) and mid-infrared (MIR) spectral regions. Salovaara *et al*. (2004; 2005) further confirm significant relationships from correlation and classification comparisons of understory indicator ferns and related species, soil conditions and spectral reflectance. Chust *et al.* (2006) obtained significant correlations between tree species composition measured from plots across the Panama Canal watershed and Landsat TM bands. However, comparisons were made from a dry season image enhancing differences observed over precipitation and phenological gradients related to deciduousness (Condit *et al.* 2000b, Santiago *et al*. 2004). Temperate and tropical studies have demonstrated that seasonal climate patterns affecting plant phenology, moisture content and leaf abscission can be exploited to enhance discrimination between certain vegetation types (Townsend & Walsh 2001; Thenkabail *et al*. 2003; Brown de Colstoun *et al*. 2003).

The level of spectral separability between upland forest types with consistent rainfall is less well known. Few studies have focused directly on evergreen rain forest canopy trees to determine the linkage between compositional dissimilarity and spectral reflectance from Landsat bands. Large stature trees provide most of the reflected electromagnetic radiation obtained from the overhead perspective of optical remote sensing instruments (Tuomisto *et al*. 2003b).

With this study, we sought to clarify the degree to which broad-scale differences in rain forest overstory trees and palms is linked to spectral differences. We compared differences among rainforest types determined from field samples taken along environmental gradients with those based on spectral reflectance obtained from Landsat TM bands. Our objectives were to 1) derive forest types from cluster and ordination analyses using tree species abundance data from plots, 2) assess the spectral “separability” or ability to discriminate among forest types, and 3) compare level of accuracy for discriminating among forest types using a “supervised” image classification and maximum likelihood algorithm

(MLA) for forest mapping with Landsat TM data. Three additional forest types were georeferenced from 151 forest patches characterized as palm swamps dominated by the species *Raphia taedigera*, tree plantations and young secondary forest re-growth to compare spectral reflectance values with those of primary forest types. Distinguishing between human modified forest types was considered important because of their structural differences and economic and ecological value (Castro *et al*. 2003).

We tested the assumption that forests types with substantially different canopy tree compositions or low statistical similarity would show significantly different spectral characteristics at the ~30m pixel scale. We expected that classification accuracy was related to the tree species similarity and level of spectral separability among forest types. Vegetation indices and other image enhancements described in methods were used to improve spectral sensitivity to differences in forest types and classification accuracy. Six different vegetation indices were compared to select a single index contributing the most to spectral separability between types.

Methods

STUDY AREA

The study area covers the 3,000 km^2 San Juan – La Selva portion of the Mesoamerican Biological Corridor (SJLS) area of privately owned remnant forest and farmland. Rapid land use change within the Corridor since colonization beginning in the 1950's has created a heterogeneous mixture of forest composition and structural types (Girot & Nietschmann 1992; Butterfield 1994; Schelhas 1996). Much of the original forest has been converted to pastures, tree plantations and agricultural production areas (Butterfield 1994). Remnant forest within the Corridor connects Costa Rica's largely protected Central Mountain Range to intact lowland rain forest located in southeastern Nicaragua (Fig. 1). Forest remnants examined occur within three life zones and two transitional zones based on the Holdridge system (Holdridge 1967). Environments within the study area are generally termed humid lowlands (<300m), foothills (300-800m) and premontane (800m-1200m) for discussion purposes. Annual rainfall averages 4000mm per year over much of the corridor, but precipitation and temperature vary with elevation and distance from the Caribbean coast. Precipitation at mid-elevation is somewhat higher and is reported to reach above 5000mm per year (Lieberman *et al*. 1996). Monthly precipitation is typically between 150 and 400mm although drier periods of <100mm of rainfall per month for one or two months a year occur in the western portion of the corridor. Weather station data obtained from the National Meteorological Institute show that lower average rainfall varies between 60 and 100mm per month during March and April west of the San Carlos River (Fig. 1). Daily temperatures average as low as 16°C above 2000m elevation and 26°C at La Selva Biological Station at 30m elevation (Sanford *et al*. 1994). Low hills or *cerros* are located amid the northern lowlands reach up to 400m in elevation and likely affect both local climate and vegetation.

Local factors associated with terrain such as soil drainage and slope stability also influence forest vegetation in the study area (Clark *et al*. 1999). Topography is extremely variable with lowland alluvial flood plains, terraces, and low hills to mountain slopes notched by steep ravines in upper elevation areas. Clark *et al*. (1999) suggest that approximately 30% of all tree species measured at La Selva Biological Station were closely correlated with specific topographic environments. Soils are generally acidic (pH ~4·5), low fertility Ultisols and Inceptisols of late Tertiary and Quaternary origin. However, soil age and development are variable depending on distance from volcanoes, lava flows, and ash falls with higher elevation soil exhibiting andesitic properties (Marrs *et al*. 1988; Sollins *et al*. 1994).

FOREST FIELD SAMPLING

Primary and lightly logged forests were extensively sampled between January and May 2003 and 2004. An adaptation of gradient-directed sampling by Sandmann and Lertzmann (2003) was used to select plot locations in forest remnants. Two assumptions were made based on previous studies: 1) tree species composition varies at the regional scale primarily along precipitation, temperature and elevation gradients (Hartshorn & Peralta 1988; Lieberman *et al*. 1996; Pyke *et al*. 2001); and 2) tree species composition varies at the local landscape scale due to local topographic factors, disturbance events or random chance (Hubbell 1979; Hartshorn 1980; Condit 1996; Clark *et al*. 1999). The first assumption was used to select sample sites consistent with our objective to observe broad- scale change in forest composition over the SJLS corridor. Soil nutrient status and physical properties, temperature and precipitation have been shown to vary with elevation (Marrs *et al*. 1988; Grieve *et al*. 1990) and contribute to changes in forest composition and structural characteristics between La Selva and the Central Mountain Range (Holdridge *et al*. 1971; Heaney & Proctor 1990). While elevation itself is not an environmental condition, it has been correlated with soil and climatic factors potentially related to changes in vegetation in the study area (Marrs *et al*. 1988; Grieve *et al*. 1990, Leiberman *et al*. 1996)). Hammel *et al*. (2004) describe vegetation changes along a precipitation gradient at lower elevations with reference to Costa Rica's extensive herbarium collections acquired throughout the northern lowlands. The second assumption was incorporated by clustering forest samples taken in fragments along the measured gradients. Plots ranged from spatially near to much greater distances to test the level of spatial autocorrelation between plots and tree species with increased distances using Mantel Correlograms (Legendre & Fortin 1989).

A total of 127 temporary 50 x 50m (0·25 ha) plots were established in forest remnants between 40m and 1200m above sea level (a.s.l.) and along a precipitation gradient from Rio Sucio to the western side of the San Carlos river (Fig. 1). Plots in lower elevation sites were located across a gradient of decreasing precipitation from areas with no pronounced dry period to those with one or a maximum of two months of <80mm of precipitation. Between two and five plots were established within forests ≥40 hectares at a minimum distance of 150m from a forest edge and 300m from the closest adjacent plot. Seven plots were established inside Braulio Carrillo National Park (BCNP) between 300 and 600m due to the scarcity or inaccessibility of primary forest remnants at these elevations. Large tree falls and canopy gaps were avoided for selecting sample sites. Tree species and diameter at breast height (dbh = 1·37m above the base) were recorded for all trees ≥30cm dbh and arborescent palms and ferns ≥10cm dbh. Diameters were estimated for some trees above buttresses and stem abnormalities that could not be reached from the ground, or a latter was used for plots with easy access. Tree identification was conducted on site by parataxonomists trained to identify a large number of trees to the species level in the study area. Unidentified trees were tagged for later identification by a returning to the plot with a local expert or by obtaining foliage samples for identification by Nelson Zamora at Costa Rica's National Institute for Biodiversity (INBio) herbarium.

Seventeen additional 25 x 25 (0·25ha) and 100 x 100m (1·0ha) permanent sample plots with dbh and full tree species identification for all individuals ≥10cm were included in the sample for a total of 144 plots. Only trees ≥30cm dbh and palms ≥10 dbh from these plots were used for vegetation analysis described below. All 144 plots were georeferenced with a Garmin GPS 12 from a canopy gap inside the sampling area with a minimum of 4 satellite signals present and ±12m positional accuracy. No field measurements were taken in palm swamps, however, 11 stands were georeferenced in the field with a GPS or located on TM images using aerial photo interpretation acquired in year 2003, 1:40,000 false color infrared photos.

Secondary forest successional stages based on Finegan (1996) and tree plantations were georeferenced using a GPS between January and May of 2004. General information was collected for secondary forests and tree plantations noting dominant tree species, developmental stage and other conditions such as the presence of dead stems and natural regeneration. Only stands of at least two hectares in size were referenced in the field with a GPS.

IMAGE PROCESSING

A Landsat TM image acquired January 14, 2001, World Reference System (WRS) path 15 and row 53, was the most recent nearly cloud free image available and was used for this study. Geometric and radiometric corrections described below were made prior to comparing ground based forest measurements with multispectral information. All image processing was done using ENVI 4·0 software (RSI 2000). To ensure location accuracy between field samples and multispectral data, the 2001 TM image was co-registered to a verified 1996 Landsat TM by Pedroni (2003) using nearest neighbor resampling with a root mean squared error (RMSE) of 2·2m. GPS locations of major highways and road intersections were collected with a Trimble GeoXT and compared to locations visible on the image as an independent evaluation spatial accuracy. Location accuracy was considered satisfactory with an estimated error of less than one half a pixel width (15m). Spectral data in Landsat TM images stored as a digital numbers were converted to reflectance values for making rigorous comparisons of spectral differences between forest types and species compositions. Therefore, TM bands 1 through 5 and 7 were converted to top of atmosphere reflectance using calibration coefficients for image dates prior to May 4, 2003 (Chander & Markham 2003). The thermal infrared band 6 was removed and not used for analyses as it has a lower spatial resolution (120m) than the other six bands (30m). Radiometric characteristics were assessed using image statistics and histograms for each band primarily to identify atmospheric scattering in the visual bands. Image quality can vary depending on regional atmospheric conditions and sensor calibration at the time of acquisition (Chander &

Markaham 2003). From our data, reflectance values offset from zero observed in histograms for bands 1, 2 and 3 in the visible wavelengths were interpreted as atmospheric scattering (Jensen 1996). An atmospheric correction was made using a dark object subtraction method and deep-water bodies from the image following methods outlined by Teillet and Fedosejevs (1995).

Radiometric quality of the image was rated as fair by the United States Geological Survey standards contained within the image metadata. Some visible sensor noise or irregular "striping" was present in the blue, green and red wavelengths, bands 1, 2 and 3 respectively. A forward and then inverse Minimum Noise Fraction (MNF) transformation was used to reduce sensor noise (Green *et al*. 1988). The MNF transformation was implemented in ENVI 4.0, which uses a modified two cascaded principal components rotation of the spectral data (RSI 2003, *also see* Li & Moon 2004). This process transformed the bands back to the original image space reducing sensor noise visually present in the image. Bands affected by noise (e.g., TM bands 1 - 3) were replaced with corrected bands in the atmospherically corrected image. The image with noise corrected bands was used for making spectral comparisons between forest types.

FOREST DATA ANALYSIS

Our main objectives were to derive forest types based on species composition and make comparisons to determine the spectral separability among types. Species importance values (IV) were used to first group plots with hierarchical cluster analysis using flexible beta linkage methods (Lance & Williams 1967) and Non-Metric Multidimensional Scaling (NMS) (Clarke 1993). Species IV for each individual species (*j*) in all 144 plots were obtained with the following equation:

$IV_j = (Relative\ frequency_j + Relative\ density_j + Relative\ dominance_j)/3$ where, density and dominance are the number of individuals and basal area per hectare respectively (Curtis & McIntosh 1950). Analyses with forest data were carried out using the PC-ORD v. 4·0 statistical software package (McCune & Medford 1999). Sorensen's Bray-Curtis coefficients (Bray & Curtis 1957; Faith *et al*. 1987) were used to create distance matrices from plots and tree species using the formula;

$$D(x_1, x_2) = \frac{\sum_{j=1}^{p} \left| a_{1j} - a_{2j} \right|}{\sum_{j=1}^{p} a_{1j} + \sum_{j=1}^{p} a_{2j}} \quad \text{where,}$$

$D(x_1, x_2)$ = is the dissimilarity between sampling unit i and species j

a_{ij} = is the abundance of species j in sample unit i

p = the total number of number of species.

We selected the default value of beta (-0·25) cluster analysis to minimize "chaining" among the clusters. A group membership variable was added to the cluster analysis to generate a second matrix for observing plots at different levels of aggregation in the cluster dendrogram (McCune & Medford 1999). For this study, we accepted clusters of plots as forest types for group members with a minimum of 25% of the information remaining according to Wishart's objective function (Wishart 1969). Forest types were assigned to each plot from cluster analysis and overlaid with plots along NMS axes. We applied NMS ordination and Monte Carlo randomizations (50 runs) with the tree data to select the number of dimensions (i.e., axes) based on the stability of the final solution using stress values below 20 recommended by Clarke (1993). Stress values are an inverse measure of fit to the data that can be used to compare multiple NMS runs with real data to runs using randomized data (McCune & Grace 2002). Pearson correlation coefficients for species and associated gradients were used to interpret factors driving the distribution of forest types along NMS axes.

Forest types determined from procedures above were expected to show a significant difference in spectral characteristics. Multi-Response Permutation Procedures (MRPP) (Mielke 1984) were used to test for a significant difference between each and every forest type using distance matrices derived from species composition and spectral reflectance values. MRPP is a nonparametric alternative to statistical methods such as Discriminant Analysis and Multivariate Analysis of Variance, thus avoiding the assumption of multivariate normality and homogeneity of variances infrequently met in ecological data (McCune & Grace 2002). Comparative analyses of forest types using MRPP are described in further detail below in addition to methods used to determine spectral separability among forest types. Similarity indices were used as a metric for observing the degree of compositional difference between forest types. Following Townsend (2000), Sorensen Bray-Curtis distance coefficients were also converted to a similarity index (SI = 1 - $D(x_1, x_2)$) as a measure of species similarity between forest types on a scale of 0 (no species in common) to 1 (the same species composition).

FOREST TYPES AND MULTISPECTRAL DATA

From each plot location, spectral data was extracted from a filtered and unfiltered image to compare separability of forest types. A texture occurrence filter with a 3 x 3 kernel size was used to calculate the weighted mean reflectance values for each center pixel from adjacent pixel neighborhoods over the entire image. This process was used to smooth abrupt changes in reflectance values that can occur due to variations in canopy shade and other low frequency noise (Hill 1999; Tottrup 2004). Two separate comparisons using procedures outlined below were made to determine differences due to image filtering.

Vegetation indices and spectral band ratios are frequently applied to characterize physiological and biophysical attributes of forest vegetation (Steininger 1996; Lu *et al*. 2004; Gitelson 2004). Vegetation indices were included in this study to assess their sensitivity to discriminate among both primary and secondary rainforest types with characteristically high biomass (Steininger 2000). Simple band ratios (e.g. TM band 4/band 5) and more complex indices in Table 1 were used to enhance discrimination among forest types while reducing effects of topography, shadows, and other background materials (Kaufman & Remer 1994; Jensen 2000). NDVI, the most commonly used index, combines the red and NIR wavelengths and is sensitive to plant biomass and leaf area (Jensen 2000). Following Lu *et al*. (2004) we also used TM band 5 (MIR) and band 3 (Red) to derive NDVI for comparison with bands typically used for NDVI (i.e., TM bands 3 and 4) to enhance its sensitivity to differences in canopy reflectance among forest types. The Soil Adjusted and Atmospherically Resistant Vegetation Index (SARVI) includes a soil calibration factor, *L,* to reduce soil brightness effects typically equal to 0.5 and gamma (γ), typically equal to 1·0, to reduce atmospheric effects (Kaufman & Tanré 1992).

The majority of our forest types are closed canopy primary forest, however recently thinned or intermediately harvested tree plantations may have substantial exposed soil. Huete & Liu (1994) showed that SARVI is an improvement over NDVI where atmospheric effects on spectral reflectance are only partially corrected. A modification of SARVI (MSARVI) includes corrections for both soil and atmosphere that were considered superior to NDVI depending on the level of prior correction (Huete & Liu 1994). Enhanced Vegetation Index (EVI) and Wide Dynamic Range Vegetation Index (WDRVI) coefficients to reduce background and atmospheric effects and were considered to improve sensitivity to the high biomass forest types (Huete & Justice 1999; Gitelson 2004). WDRVI essentially extends the range of values that may reach saturation or maximum values in high biomass vegetation with other indices such as NDVI (Gitelson 2004). Separability tests comparing the forest types were performed using each of the 6 indices in Table 1 to identify which of them contributed most to detecting spectral differences between the forest types. The index demonstrating the greatest separability enhancement was then incorporated as an additional band for image classification using MLA.

MULTISPECTRAL DATA ANALYSIS

Two types of comparisons were made to examine the multispectral spectral separability among the derived forest types. For the first approach we used paired MRPP comparisons to test the null hypothesis that forest types are no different in species composition and spectral reflectance. A matrix of Euclidean distance coefficients for plots and spectral reflectance values was calculated for MRPP tests. Non-metric MRPP converts the distance matrix, from forest types and spectra from Landsat TM bands in this case, to ranks before calculating a test statistic (McCune *et al*. 2000). The agreement statistic *A*, used in MRPP, describes the likelihood that an observed difference between forest types is high for reasons greater than chance and is independent of sample size (McCune & Grace 2002).

A second approach was used to assess multispectral separability of forest types using the M statistic (Kaufman & Remer 1994; Pereira, 1999) and Jeffries-Matusita (JM) distance (Trigg & Flasse 2001). The M statistic was applied to determine separability among forest types for individual TM bands and each of the 6 vegetation indices. It assesses separability between two sample class distributions using the mean and standard deviation values to effectively measure the signal (mean) to noise (standard deviation) ratio:

$$M = (\mu_A - \mu_B)/(\sigma_A - \sigma_B)$$ where,

μ_A= the mean reflectance value of forest type A,

μ_B= the mean reflectance value of forest type B,

σ_A= the standard deviation values for forest type A,

σ_B= the standard deviation values for forest type B.

Absolute values of M>1 indicate good separation and values close to 0 indicate poor separability. We also summarized M statistics for each band and index for the filtered and non-filtered image to assess its potential as an enhancement for distinguishing among forest types. JM distance was used to assess multivariate spectral separability among forest types using all bands simultaneously:

$$JM_{ub} = \sqrt{2(1-e^{-\alpha})}$$

$$\alpha = \frac{1}{8}(\mu_u - \mu_b)^T \left(\frac{C_u + C_b}{2}\right)^{-1} (\mu_u - \mu_b) + \frac{1}{2}\ln\left[\frac{\frac{1}{2}\left|C_u + C_b\right|}{\sqrt{\left|C_u\right| \times \left|C_b\right|}}\right]$$ where,

u and b = the two region classes,

Cu is the covariance matrix of u,

μ_u is the mean vector of u,

T is the transpose function.

JM distance is often used to evaluate and visualize separability using more than 2 spectral bands and to refine spectral information used as training information for supervised image classification (Trigg & Flasse 2001). This method provides an index between 0 and 2·0 where large values indicate well-separated classes. Forest types, or other response categories, showing a JM distance higher than 1·7 are considered well separated (RSI 2003). JM distances among forest type categories were then compared with significantly different forest types based on MRPP tests. Bonferroni-corrected alpha values (α = 0·05 and 0·01) were applied to adjust the experiment wise error rate using α/*k* where *k* equals the number of total comparisons. These methods are commonly applied to response categories in remote sensing applications and were contrasted with the MRPP comparisons using both species composition and spectral information as MRPP statistics have not been previously used to assess spectral differences among vegetation categories.

Spectral reflectance values were extracted from the corrected and filtered TM image for each forest type and plot location using two methods. First, spectral reflectance values for each band were taken directly from each plot location (i.e., a single pixel) on the TM image for comparisons using MRPP statistics. A larger set of pixels were selected for comparisons with M statistics and JM distance metrics over representative plot locations of each forest type. Spectral information was taken from 25 pixels (2 hectares) over a plot location with a total of 75 to 450 pixels for each forest type. The range in number of pixels was dependent upon the number of plots available within a class. A minimum of 3 plots in a forest type was used to make separability comparisons (i.e., 3 plots = 75 pixels). Spectral data were only selected from locations where shadow or edge pixels from adjacent land cover types could be avoided. We assumed that pixels taken for comparison from a forest remnant with plots classified as the same forest type were spatially autocorrelated with other nearby forest in terms of species composition. Mantel Correlograms (Legendre & Fortin 1989) were used to test the assumption that species are positively and significantly autocorrelated over relatively short distances using Sorensen's Bray-Curtis dissimilarity coefficient and tree species IVs from georeferenced plots. Correlograms were computed using the PASSAGE v. 1·1 spatial statistics package (Rosenberg 2001) by creating a distance class matrix from coordinates for each plot. A matrix using Euclidean distance of plot elevation, average annual temperature and annual precipitation from a 90m digital elevation model (DEM) and WorldClim ~1 km climate surfaces (Hijmans *et al*. 2005) were also plotted against species with the Correlogram.

ACCURACY ASSESSMENT

As a practical test of our separability analysis, we used our plots to perform a supervised classification with MLA of forest types based on our separability assessment. One set of pixels from plot locations was used as training information to classify each forest type and a second set of pixels from separate plot location was used to assess accuracy (validation pixels). Accuracy assessments for remote sensing applications compare response categories to ground reference data to assess accuracy of a final map product (Congalton & Biging 1992; Congalton & Green 1993). Error (or confusion) matrices and agreement statistics were used to quantify overall percent accuracy among land cover categories and for each individual class (Congalton & Green 1999). Summary statistics such as overall percent agreement, percent agreement for each class and the Kappa coefficient (Cohen 1960) were used to summarize accuracy for all forest types used in the image classification (Congalton & Green 1999). Producers and users accuracy were calculated for each individual class. Producer's accuracy is the total number of correctly classified pixels divided by the total number of validation pixels and user's accuracy is the total number of correctly classified pixels divided by the total number of pixels in a forest type. The Kappa coefficient is the chance corrected proportional agreement and ranges between 1 (perfect agreement), 0 (no agreement above that expected by chance) and -1 (total disagreement):

$$k = \frac{N\sum_{i=1}^{r} X_{ii} - \sum_{i=1}^{r}(X_{i+} \cdot X_{+i})}{N^2 - \sum_{i=1}^{r}(X_{i+} \cdot X_{+i})} \quad \text{where,}$$

R is the number of rows in the error matrix,

X_{ii} = the number of observations in row I and column x,

X_{i+} = the total number of observations in row i,

X_{+i} = the total number of observation within the matrix,

N = the total number of observations within the matrix

These statistics provided a summary of classification accuracy at different levels of aggregation of forest types from cluster analysis useful for evaluating the overall quality of a final map product. Each forest type was classified based on their spectral characteristics that could be further aggregated according to accuracy estimates. We used a hierarchical approach to combine classes into the next level, aggregating forest types based on confused classes and group membership from cluster analysis. A majority filter with a 3x3 moving window was used prior to accuracy assessment to reduce scattered individual pixels.

Results

PRIMARY FOREST TYPES

From the primary forest plots, 462 tree species were identified, 95% to genus and 91% to the species level. Morphospecies were used for trees identified to the genus level by giving them a descriptive species name based on taxonomic features and later a species number used during analyses. Only tree species encountered on more than one plot, 203 species total, were used to derive forest types with cluster analysis and NMS ordinations. Only seven percent of tree species used in the analysis were morphospecies.

Cluster analysis of forest plots resulted in nine forest types by selecting groups with close to 25% or more information remaining from the cluster dendrogram and group membership matrix. We characterized each forest type using tree species with the highest percent IV (Table 2) and by elevation range (Fig. 2). We will refer to forest types by their Table 2 abbreviations and briefly discuss factors and species driving the classifications from cluster analysis. We used the group membership matrix derived from the cluster analysis to overlay forest types with NMS ordination plots for interpretation.

Ordination of plots and tree species resulted in a 3 dimensional solution with a final average stress level of 17·4 ($p = 0{\cdot}024$). Axis 1 explained 44% of the variation and axes 2 and 3 explained and additional 38% of the variance. Axis 1 was interpreted as a strong relationship between elevation and forest types. Nearly all plots from lowland forest types were to the left of the ordination plot and foothills and premontane forest types to the right along axis 1 (Figs. 3a and 3b). Correlation between elevation and axis 1 was highly positive using the Pearson correlation coefficient ($r = 0{\cdot}87$) and plot elevations taken from a 90m digital elevation grid (DEM). Change in species composition represented by plots descending axis 2 were interpreted as a gradient of decreasing rainfall extending from the Caribbean coast inland (Fig. 3a). Axis 2 showed the strongest correlation with total precipitation from plot locations during the driest month ($r = 0{\cdot}50$) and total annual precipitation ($r = 0{\cdot}36$). Precipitation information was taken from interpolated grids using weather station locations and records in the corridor area. Axis 3 was less interpretable although it showed a high negative correlation with annual precipitation ($r = -0{\cdot}35$). Axis 3 was useful to classify two plots taken in the most western forest type (Dg) where axis 3 values approach 100 and both annual and monthly precipitation were the lowest among plots (Fig. 3b).

Three lowland forest types were primarily characterized by a decreasing abundance of *Pentaclethra macroloba*, a mid to upper canopy tree species common to lowland forests in the study area. Distinguishing characteristics among these types were the extreme abundance of *P. macroloba* in the Pc forest type and highly abundant palm species in the Pp type. The Pd type appeared to be a transition from *P. macroloba* dominated forests to western forest types comprised of differing species. The Qp and Dg lowland forest types were characterized by increasingly abundant canopy trees *Qualea paraensis*, *Dipteryx panamensis* and *Dialium guianense* respectively*,* and a low abundance or absence of *P. macroloba* in upland forests west of the San Carlos River. Transitional areas among lowland species compositions were clearly represented along axis 2 overlaying forest types with ordination plots (Figs. 3a and 3b). *P. macroloba* was highly and positively correlated with axis 2 (r = 0·59) and *Q. paraensis* highly and negatively correlated with axis 2 (r = -0·57). The Dg type was characterized by tree species *Dialium guianense, Brosimum alicastrum* and *Sclerolobium costarricense* showing a much higher abundance of these species in plots furthest west. The three foothills forest types showed a transition from lowland forest types with the absence of *P. macroloba* and greater variety canopy trees between 275 and 300m elevation. Species characteristic of the foothills and premontane forest types such as *Vochysia allenii*, *Macrohasseltia macroterantha*, *Conostigia rufescens*, *Pterocarpus rohrii*, *Guarea bullata* and *Cyathea spp.* were also positively correlated with axis 1 ($r \geq$ 0·40). The most conspicuous changes in vegetation were a decrease in palm species and an increase in tree fern abundance at elevations above 800m (*also see* Lieberman *et al.* 1996). The premontane forest type, Cy, showed a striking abundance of *Cyathea spp.* and an increase in the abundance and number of *Guarea* species. Species composition and turnover recorded from plots and forest types closely match plot descriptions from Hartshorn and Peralta (1988) and Lieberman *et al.* (1996) for these elevations.

Mantel Correlograms indicated that spatially dependant patterns of both species and measured environmental gradients matched closely. Species compositions were significantly autocorrelated among closely spaced plots that gradually diminished with increased inter-plot distances as did environmental conditions (Fig. 4). The shape of spatial autocorrelation between increasingly distant plots observed from the Correlogram was analogous to an environmental gradient, though geographic distance can also account of compositional differences at this scale. Forest compositions were most highly and positively autocorrelated at ≤3 km (Mantel r = 0·11, p < 0·0001) similar to distances reported by Pyke *et al*. (2001) for lowland Panamanian forests at 5 km. Plots located in small *cerros* across the lowlands that showed significant autocorrelation with species in the foothills environment of the central mountain range at 22 to 25 km away however plots were significantly autocorrelated up to

~15 km. Correlation among plots and species became significantly negative at distances >40km (Mantel $r = 0{\cdot}10$, $p < 0{\cdot}0001$) indicating low species similarity for plots at these distances. These results suggest that plots closer together were more likely to have similar vegetation compositions and potentially similar spectral reflectance values.

Paired comparisons of plots grouped by nine forest types with MRPP tests resulted in highly significant differences at $\alpha = 0{\cdot}001$ (Bonferroni corrected $\alpha = 0{\cdot}000027$) for all but the Dg forest type. The Dg forest type was not significantly different from all other types likely due to its small sample size (i.e., 2 plots) and reduced statistical power for making multiple comparisons. Similarity indices between the Dg forest type and all others were low ($\leq 0{\cdot}26$) (Table 3). We considered a SI >0·50 to be high similarity that was observed between forest types dominated by *P. macroloba*.

As our primary objective was to study the spectral separability of forest types we also considered 6 aggregate forest types by combining group members based on the most abundant canopy tree species. Aggregating plots using the group membership matrix resulted in combining types with the highest abundance of *P. macroloba* in the lowlands and Va and Ma foothills types. The Va and Ma forest types covered nearly identical elevation ranges and were more closely related in terms of tree species, particularly *Vochysia allenii*. Each of these forest types showed similarity indices close to or >0·50 and somewhat aggregated plot clouds along ordination axes 1 and 2 (Fig. 3b). We discuss these below as a part of image classification and accuracy assessment.

SECONDARY FORESTS AND TREE PLANTATIONS

A total of 73 secondary forest stands including abandoned forest plantations dominated by natural regeneration were georeferenced. From these observations, most secondary stands we encountered were between an early successional stage (52% of points) dominated by a mixture of regenerating shrub and trees species or a mid-successional stage with greater abundance of tree species (33% of points). Later successional forests were scarce (15% of points) and covered relatively small areas consistent with previous studies in the region (Guariguata *et al*. 1997; Read *et al*. 2001). In many cases later successional forest turned out to be highly disturbed edges adjacent to what we have referred to as primary forests. These areas were not georeferenced as they were generally less than two hectares. Secondary forests >2 ha were in fact difficult to locate in the corridor and many were formerly tree plantations overtaken by natural regeneration. A total of 67 tree plantations considered productive (i.e., very few dead trees with a single tree species canopy) were referenced with 50% the points represented by exotic tree species *Gmelina arborea*. The remaining 50% of plantations encountered were comprised of native tree species *Hyeronima alchorneoides* (12%) and *Cordia alliodora* (6%) and exotic *Terminalia ivorensis* (10%) among other less frequent species.

No comparisons of species composition were made among secondary forest or plantations because quantitative information was not collected from these types. Furthermore, only two combined classes were used to determine their spectral separability from primary forest types; secondary forest was classed as natural forest “re-growth” (Rg) and established tree plantations classed as “reforestation” (Re) for spectral comparison with all primary forest types combined.

SPECTRAL SEPARABILITY OF FOREST TYPES

The M statistic was used to first compare each vegetation index and TM band’s contribution to spectral separability among the 8 primary forest types and 3 additional types for both the filtered and non-filtered image. In all cases the filtered image enhanced separability among forest types showing a 33% increase in average M values for each spectral band and index (Table 4). Average M values greater than 1 increased by 23% on average and generally increased the number of comparisons considered well separated (i.e., $M \geq 1$). Therefore, all further comparisons were conducted with the filtered image.

Landsat bands 1 and 3, the blue and red bands, contributed most to separability among forest types (Table 4). Approximately 50% of the 55 comparisons were well separated for the first three TM bands with decreasing separability in the NIR and MIR bands. The blue, green and red wavelengths are most susceptible to atmospheric scattering, but are also sensitive to plant chlorophyll absorption and differences in canopy structure (Jensen 2000). Of the visual bands, the red band with longer wavelengths is considered least susceptible to scattering and showed relatively high contrast among forest types (data not shown). Contrast among forest types appeared to be greatest for the red, NIR and MIR spectral bands particularly among forest composition associated with high and lower elevation sites. However, vegetation indices using a combination of the Red and NIR bands showed the highest average M and the greatest number of comparisons considered well separated (Table 4). Vegetation indices ND3, WDRVI and NDVI were most sensitive to differences in forest composition overall among the forest types. Of these, WDRVI and NDVI showed the highest M values for separating tree plantations from natural regeneration although they were below the separability threshold (M = 0·87 and 0·84, respectively). Regenerating areas and tree plantations were among the two most difficult forest types to discriminate from any single band or index. Overall WDRVI or NDVI alone showed the greatest discrimination among forest types in 55% of the cases compared. More complex vegetation indices incorporating the blue band to reduce background effects of canopy shadow and soil showed the least separation among forest types. These indices also had similar, but lower M values for tree plantation and natural forest regeneration (0·75 and 0·82).

To interpret comparisons of forest types on a case-by-case basis, we used M values from NDVI comparisons, JM distance and MRPP tests where all six TM bands were included. NDVI was used to make comparisons because it showed the highest average M and was second highest in the total number of comparisons resulting in values >1 (Table 4). Therefore, we included NDVI as an additional band for JM and MRPP comparisons because it enhanced separability by 6% when compared with JM values from only the six spectral bands. NDVI also showed a 10% increase in JM values for separating tree plantations and natural regeneration and a 5% increase over WDRVI when included as an additional band.

Resulting M values with NDVI alone compared relatively well with the level of compositional similarity among forest types in Table 3. Forest types showing similarity indices >0.40 were poorly separated in all cases and high M values (i.e., well separated forest types) were associated with low similarity in species composition among primary forest types in all but a few comparisons. The highest elevation forest type (Cy) that was characterized by abundant arborescent ferns *Cyathea spp.* and trees of the genus *Guarea* had low similarity with lowland forest types (SI <0·2) resulting in high M values between 1·7 and 4·0 (Table 5a). Similarity indices among higher elevation forest types did not follow this pattern for comparisons with NDVI. The Cy forest type was not spectrally separated from Ma, Ta or Va forest types although tree species similarity indices were very low (SI = 0·07 - 0·12). M values comparing each individual TM band among these types were also lower than 1 in nearly all cases. Palm swamps, tree plantations, and to a lesser extent regenerated stands were considered simplified in terms of forest canopy structure and species compositions (i.e., uniform and few or only one tree species) in comparison with primary forest types. However, spectral comparisons among these and lowland primary forest were not well separated using a single vegetation index.

Forest type comparisons using all spectral bands were expected to be significantly different particularly among types with low similarity indices. A total of 55 paired comparisons with all 11 forest types resulted in 42 that were significantly different based on MRPP tests and 39 with a JM distance ≥ 1·7 (i.e., well separated) (Table 5b and c). Of the 28 comparisons made for the 8 primary forest types, 17 of these were significantly different at $\alpha = 0{\cdot}05$ and 11 at $\alpha = 0.01$ using all TM bands (Table 5c). Thus, significant compositional differences among the forest types resulted in significantly different spectral characteristics in many cases. Forest types with similarity indices <0.36 were generally well separated and those >0·40 were poorly separated despite significant differences in species composition. Quite clearly the 3 forest types dominated by *P. macroloba* were not well separated from one another. Some notable exceptions were among the premontane forest type (Cy) and the more heterogeneous Ma and Ta foothills forest types. These types were not found to be significantly different spectrally although they showed very low compositional similarity. The low number of plots and spectral information used for comparisons with the Cy type likely reduced our ability to detect these differences with MRPP tests using spectral data.

No quantitative information on species composition was available to compare palm swamps with other forest types, but they were spectrally well separated from most forest types with the exception of the Qp and Pd types. Predominantly single species palm swamps could be visually identified on Landsat TM color composite images although numerous small patches amid forest canopies were less discernable. The Qp and Pd forest types characterized by abundant palms and tree species such as *Qualea paraensis*, *Dipteryx panamensis* and *P. macroloba* were at the lowest elevation sites and often interspersed with palm swamps inhabiting small topographic depressions in these stands. Palm swamps encountered during field sampling were less evident on the TM image and often covered only a few hectares. Thus, pixels selected from other palm dominated forest types potentially contained similar spectral information. The same source of error likely occurred with comparisons between tree plantations and regenerating forest types. Natural forest regeneration was frequently dominated by *P. macroloba* or *Vochysia ferruginia* in low elevation secondary stands where most forest re-growth areas occurred. The Qp forest type was largely dominated by tree species in the Vochysiaceae family that comprise 17% of the basal area per hectare in our plots. *P. macroloba* represents nearly 40% of the basal area per hectare in the Pp forest type. Each of these species tends to dominate forest canopies in young successional stands and primary forest vegetation. Lower spectral separation between these forest types appeared to be related to canopy tree compositions.

IMAGE CLASSIFICATION AND ACCURACY

Accuracy assessment for the supervised classification using all 11 forest types produced results parallel to the separability tests. Overall accuracy was low (63% overall, Kappa = 0·59) given that some poorly separated classes were used as training data for image classification (Table 6a). Lowland forest types dominated by *P. macroloba* showed the greatest misclassification errors when subdivided into the 3 separate forest categories (25 – 75% misclassification error). A few of the classes we previously considered less separated such as palm swamps and the Qp forest type showed somewhat higher classification accuracy than expected, as did the Cy forest type. In most cases, JM distance among comparisons above 1·5 resulted in a higher percentage of correctly classified pixels. Regenerating natural forests and tree plantations were close to this threshold (JM = 1·49) and showed classification accuracy at 72% producer's accuracy and ≥78% percent user's accuracy. Accuracy estimates from error matrices strongly reflected prior separability tests except where we had a low number of samples for comparisons.

To determine accuracy in a hierarchical fashion, we combined all three lowland *P. macroloba* forest types, the Ta and Va foothills types and all foothills forest types thereby forming seven forest types. These were essentially nested forest types based on group membership from hierarchical cluster analysis and their level of class separability. Aggregating classes improved overall accuracy to 77% at 8 classes and 81% at 7 classes with Kappa coefficients of 0•73 and 0•77 respectively (Table 6b and c).

Discussion

Our objective to derive forest types from plots sampled along environmental gradients showed vegetation patterns reported from previous vegetation studies. The forest types and abundance patterns were similar to those previously reported in forests between La

Selva and the Central Mountain Range (Hartshorn & Peralta 1988; Hartshorn & Hammel 1994; Lieberman *et al*. 1996). Species dominating swamp forests described by Webb and Peralta (1998) and Lieberman *et al*. (1985) were comparable to the Pc forest type we have identified from different locations, but on similar sites. Seasonally inundated forests are commonly identified by characteristic tree species, *P. macroloba*, *Carapa guianensis* and *Pterocapus officinalis* that can make up as much as 70% of the basal area (Webb & Peralta 1998). The Pc forest type was distinguished from the Pp type by the overwhelming dominance of *P. macroloba* and lower abundance of arborescent palms. Our broad distribution of plots was not designed to investigate hillslope positions, however a greater abundance of palm species for the Pp and Qp types were typical of hilly terrain and alluvial terraces (*also see* Clark *et al*. 1995). Species elements of the lowland Qp type we observed were also discussed by Hammel *et al*. (2004) indicating an abundance of four species in the Vochysiaceae family and occurrence of some rare trees such as *Podocarpus guatamalensis* for the San Carlos area. Other widely recognized timber species such as *Vantanea barourii* and *Vatairea lundellii*, "Cocobolo de San Carlos", were characteristic of the Qp type, but in somewhat lower abundance potentially due to timber extraction from some sites. We considered the Qp forest type to be unique in species composition compared with other lowland forests with the exception of the Pd type that appears as a transition between *P. macroloba* and Vochysiaceae dominated forests. The Qp showed a low species similarity value with the Pc type (Table 3) that, in general, occupy the western and eastern lowlands respectively. The Holdridge Life Zone system, that uses annual precipitation and temperature values to delineate lowland forest environments, groups each of these forest types into a single humid lowland tropical forest category.

Change in tree species composition follow an elevation and temperature gradient with near complete turnover in canopy species between the low elevation sites and 1000m, also noted by Lieberman *et al*. (1996). Lieberman *et al*. (1996) point out that tree species tend to show individualistic behavior along such gradients and discrete life zones cannot be recognized on the basis of species composition. Overstory trees did appear to inter-grade along measured gradients that were reflected by similarity values from our plots (Fig. 2), though we often found the same species reported from comparable elevations by Hartshorn & Peralta (1988), Lieberman *et al.* (1985) and Lieberman *et al*. (1996). Individual trees species such as *V. allenii* were abundant at elevations exceeding 400m and, curiously, also found abundant again in plots close to the San Carlos River below 100m (i.e., showing a bimodal distribution). Other species such as *Brosimum lactescens* and *Iriartea deltoidea* were occasionally to frequently abundant on plots over the range of elevations sampled apart from the very highest elevation sites. Topographic or other edaphic factors and the broad amplitude of some palm species, such as the palm *I. deltoidea* have also been reported from Amazonian plots ((Ruokolainen & Vormisto 2000; Pitman *et al*. 2001). Palms appear to be habitat generalists for the lowlands and foothills at the scale of our measurements, though abundance and the number of palm species present were indicative of soil drainage conditions (Clark *et al*. 1995).

Our second objective to assess the spectral separability of forest types, which is importance for broader scale mapping, showed that significant compositional differences among types often corresponded to spectral differences in Landsat TM images. Separability is naturally dependent upon the spatial, spectral and radiometric resolution of imagery, but also appeared to be related to tree species dominating the upper forest canopies. Important differences among forest types, such as low compositional similarity, were generally well separated at the resolution of Landsat TM data. Spectral differences among composition classes were also noted among temperate broadleaf forests by Townsend (2000) where similarity indices were <0·50. Our comparison of *P. macroloba* forest types at a SI close to this value often resulted in lower or non-significant spectral separability. Therefore, significant differences in species composition among forest types may not constitute well-separated categories where forest canopies are dominated by a few of the most common species. As evidence, the Pp and Pc types were significantly different in species composition yet were among the most highly similar and confused categories from our classification accuracy assessment. Conversely the Pp and Ta types were compositionally similar (SI = 0·45), but were not highly confused from accuracy assessments with the absence of *P. macroloba* from the Ta type.

Comparisons among forest types with species-rich or heterogeneous forest canopies were relatively well separated from *P. macroloba* dominated types. However, lower species similarity did not result in significant spectral differences from comparisons between the Cy and Ta, Va and Ma forest types. These were difficult forest types to access in our study area, which partially limited the number of plots available for making spectral comparisons. The foothills types were also highly transitional and produced rather low classification accuracy until combined into a single class. In the lowlands, the Qp type was spectrally distinct from all other forest types with few exceptions. The high abundance of palms and more numerous palm swamps are suspected to have produced lower separability for the Ra and the Pd type. However we achieved 79% producers and 65% users accuracy in this category, indicative of its lower compositional similarity with most other forest types.

Our comparison of image enhancements and vegetation indices indicated that these techniques also improve detection of tropical forest types. Efforts to reduce sensor noise and atmospheric effects are standard procedures for remote sensing studies of vegetation. Yet, less commonly applied methods such as MNF transformations and spectral filtering to reduce sensor and other background noise proved useful for increasing separability among forest types. The filtered image showed a substantial increase in M and JM values over the non-filtered image as well as the number of forest types considered well separated. We achieved improved separability of forest types similar to comparisons made by Tottrup (2004) who applied a spectral filter with increasingly larger kernel sizes for discriminating forest types in north-central Vietnam. Larger kernel sizes were not applied for pre-classification image filtering with this study because of the highly fragmented and heterogeneous forest conditions of our landscape.

Comparisons of each forest type with individual spectral bands and vegetation indices were also instructive for making decisions on which of these may be incorporated into image classification. We found that NDVI met our objective to a greater degree than other indices for discriminating among some of the most poorly separated forest types such as forest re-growth and tree plantations. This may be attributed to the increased sensitivity of vegetation indices using the Red and NIR bands to changes in leaf area index and other forest structural characteristics as noted in previous studies (Steininger 2000; Lu *et al*. 2004; Gitelson 2004; Pocewicz *et al*. 2004). However, forest re-growth and tree plantations were still among the most difficult forest types to differentiate from one another according to all of the comparisons we made. Overall, NDVI improved separability among all forest types by 6% on average according to JM distance and by 10% in the case of forest re-growth from tree plantation forests when incorporated with the other 6 TM bands. These figures represent a substantial gain in sensitivity that contributed to classification accuracy in these types at 72% producer's accuracy and 78 to 90% user's accuracy (Table 6a and 6b).

Our approach to forest classification enables easy aggregation when forest types must be combined to improve accuracy. At lower levels of aggregation we sacrifice accuracy for a more precise forest classification according to our error matrices and summary statistics. At the highest level of aggregation we essentially define forest and non-forest types that may be most accurate, but have lower practical value for identifying forest habitats of interest to conservation managers (Fig. 5). Each of the two classification levels of Figure 5 presents a trade off between accuracy and loss of information that will affect their utility for decision making. For some applications, classification accuracies between 77 and 81% may be a sufficient level of accuracy.

The result of our classification with MLA at this level indicates a heterogeneous mixture of forest types in the corridor. We found a greater number of forest plantations in locations not surveyed during our field sampling that were verified using 2003 aerial photos. However, some sunlight affects illuminating steep hillsides were a considerable source of error where native forests were sometimes misclassified as tree plantations. These obvious sources of error did not enter into the error matrix or accuracy assessment, as we had no verification data from such sites. Other agroforestry systems or citrus tree groves with substantial tree cover may also be confused with other forest types. We considered our comparisons a preliminary classification that suggests additional corrections are necessary to generate accurate quantitative estimates of some forest types. Sun illumination corrections incorporating a digital elevation model may improve forest classification in these areas, however a DEM of sufficient resolution and vertical accuracy is needed (Fahsi *et al.* 2000, Castro *et al*. 2003) that is currently unavailable. Nevertheless, use of globally available elevation or terrain variables from the 3 arc-second (90m) Shuttle Radar and Topography Mission (SRTM) could enhance predictive classification methods. Decision tree models to incorporate ancillary variables in place of the maximum likelihood algorithm will be evaluated in subsequent work.

Some constraints to the quantitative approach we have taken to establish forest classes and generate training data is that it requires ground based forest measurements. The cost of establishing plots for habitat classification and access to remote sites is limiting in most all situations. However, placing a smaller number of plots along ecological gradients as we have done presents a potential solution for minimizing costs when more detailed forest classification is an objective. Our reduced sampling method using temporary 0.25ha square plots and a higher diameter limit for tree measurements was relatively rapid to implement with few materials involved. The increased availability of elevation and climate data sets can greatly facilitate locating plots or transects in strategic parts of the landscape to observe large scale differences in vegetation. We estimate that the challenge of identifying so many tropical tree species is reduced by more than half with a 30cm dbh limit in some of our most species rich forest types. A team of 2 to 4 people can install 2 to 3 plots a day following our protocols although this greatly depends on access to sites. Alternatively, more homogeneous forest compositions or structural classes can be identified with much reduced sampling. Forest types such as tree plantations and palm swamps and, to a lesser extent secondary forests could be referenced in the field with a GPS or taken from aerial photos for classification purposes depending on objectives.

Conclusions

The Central American isthmus is replete with environmental gradients that influence species compositions sometimes over relatively short distances. Integrating vegetation studies along such gradients with remotely sensed data showed enhanced forest classifications in these complex environments. Differences in tree species compositions over the gradients we measured were readily observed at the scale of our data and closely match those reported from other botanical studies in the region. Efforts to characterize diverse habitats in tropical environments can combine multivariate techniques to organize tropical vegetation data into biologically meaningful categories to compare their spectral separability. We have used procedures to define and compare forest classes of interest that were accomplished fairly rapidly prior to image classification. Separability tests are standard procedures in remote sensing applications as are cluster analyses and ordination techniques in community ecology. These two approaches are closely linked for identifying forest types in priority conservation areas and observing changes in forest characteristics. Our analysis showed that differences in forest compositions over these gradients can be detected at the scale of Landsat TM imagery. From our preliminary assessment, we believe that the Qp forest type represents a habitat type that is not currently within Costa Rica's extensive system of national parks.

Human activities have dramatically altered the spatial arrangement and conditions of these and other Mesoamerican forest habitats. Discriminating f highly modified forests such as natural re-growth and tree plantations from remnant old-growth forest was also greatly enhanced by selecting NDVI over other vegetation indices to meet our objectives. We have only minimally addressed other ecological gradients such as forest successional changes. Tree plantations and secondary re-growth in the study area were more heterogeneous in species composition, stand structure and production status than at the level of our classification. These should also be the focus of future investigations as a method of tracking regional reforestation programs and sustainable forest management efforts in support of biological corridors.

The forest types we detected at the scale of Landsat TM data present strata or levels of connectivity suitable for researching other ecological questions. Determining the role of forest plantations and secondary forests to facilitate species movement among forest remnants is a key question in this and other corridor areas. Integrating these aspects into characterization and mapping of tropical forests would likely aid conservation activities, sustainable forest management, and research within proposed corridor areas.

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Tables

Table 1. Vegetation indices formulas derived from Landsat TM data and spectral bands. Equation symbols and coefficient values include; r= *values are reflectance*, $P*$= *values have partial atmospheric correction*, $a=0.20$, $\gamma = 1.0$, $C_1=6.0$, $C_2=7.5$, and $L=1.0$ according to the references provided.

Vegetation index	*Equation*	*Reference*
Normalize Difference Vegetation Index	$NDVI = \frac{rNIR - rRed}{rNIR + rRed}$	Rouse et al. 1974
ND53	$ND53 = \frac{rMID5 - rRed}{rMID5 + rRed}$	Lu et al. 2004
Wide Dynamic Range Vegetation Index	$WDRVI = \frac{a * rNIR - rRed}{a * rNIR + rRed}$	Gitelson 2004
Enhanced Vegetation Index	$EVI = \frac{P * NIR - P * Red}{P * NIR + C_1 P * Red - C_2 P * Blue + L}(1 + L)$	Huete and Justice 1999
Soil and Atmospherically Resistant Vegetation Index	$SARVI = \frac{P*_{rNIR} - P*_{rb}}{P*_{rNIR} + P*_{rb} + L}$ $P*_{rb} = P*_{rRed} - \gamma(P*_{rBlue} - P*_{rRed})$	Huete and Liu 1994
Modified Soil and Atmospherically Resistant Vegetation Index	$MSARVI = \frac{2P * rNIR + 1 - \sqrt{[(2P * rNIR + 1) - \gamma(P * rNIR - P * rb)]}}{2}$	Huete and Liu 1994

Table 2. Primary forest types identified in the SJLS Biological Corridor and the number of plots representing each one in order of decreasing elevation. Average importance values (IV) are used to indicate the dominant tree species for each forest type. The (Pm) abbreviation indicates *Pentaclethra macroloba*-dominated forest types.

Abbreviation	**Environment**	**Dominant species**	**Ave. IV**	**No. plots**
Cy	Premontane	*Ferns - Cyathea spp.*	20	3
		Guarea spp.	8	
		Pterocarpus rohrii	6	
		Pouteria sp.	6	
		Conostegia rufescens	6	
Ma	Foothills	*Palm - Iriartea deltoidea*	9	9
		Apeiba membranacea	4	
		Vochysia allenii	4	
		Tapura guianensis	3	
		Pterocarpus rohrii	3	
		Maranthes panamensis	3	
Va	Foothills	*Vochysia allenii,*	7	13
		Palm - Euterpe precatoria	5	
		Stryphnodendron microstachyum	4	
		Pourouma bicolor	3	
		Guarea bullata	3	
		Macrohasseltia macroterantha	2	
Ta	Foothills	*Palms - Euterpe predatoria, Socratea exorrhiza, Iriartea deltoidea*	16	12
		Tapirira guianensis	7	
		Dendrobangia boliviana	3	
		Carapa guianensis	3	
		Minquartia guianensis	3	
Pp (Pm)	Lowland/Foothills	*Pentaclethra macroloba*	23	53
		Palms - Welfia georgii, Iriartea deltoidea, Socratea exhorriza, Euterpe predatoria	23	
		Tetragastris panamensis	2	
		Carapa guianensis	2	
		Licania affinis	2	
Pc (Pm)	Lowland	*Pentacletra macroloba*	38	18
		Palms - Welfia georgii, Socratea exorrhiza	10	
		Carapa guianensis	4	
		Dendropanax arboreus	3	
		Apeiba membranacea	3	
		Dialium guianense	2	
Pd (Pm)	Lowland	*Palms - Euterpe predatoria, Welfia georgii, Iriartea deltoidea, Socratea exhorriza*	25	10
		Pentaclethra macroloba	11	
		Licania affinis	4	
		Elaeoluma glabrescens	4	
		Dipteryx panamensis	3	
		Qualea paraensis	3	
Dg	Lowland	*Dialium guianense*	12	2
		Apeiba membranacea	5	
		Sclerolobium costarricense	4	
		Brosimum alicastrum	4	
		Pourouma bicolor	4	
Qp	Lowland	*Palms - Welfia georgii, Socratea exhorriza, Euterpe predatoria, Iriartea deltoidea, Prestoea decurrens*	29	24
		Qualea paraensis	5	
		Dipteryx panamensis	5	
		Dialium guianense	4	
		Vochysia ferruginea	4	
		Couma macrocarpa	3	
Ra	Lowland	*Raphia taedigera*	-	11

Table 3. Average similarity index among primary forest types from Sorensen's Bray-Curtis dissimilarity coefficient. Similarity index is calculated as SI = 1- $D_{(x_1, x_2)}$ with values close to 0 having fewer species in common with another forest type and values closer to 1 with more species in common.

Type	**Pc**	**Pp**	**Qp**	**Pd**	**Ma**	**Cy**	**Ta**	**Va**	**Dg**
Pc	-								
Pp	0·59	-							
Qp	0·27	0·51	-						
Pd	0·36	0·56	0·58	-					
Ma	0·16	0·26	0·19	0·15	-				
Cy	0·01	0·02	0·01	0·01	0·13	-			
Ta	0·28	0·45	0·37	0·36	0·38	0·07	-		
Va	0·28	0·30	0·22	0·21	0·44	0·12	0·45	-	
Dg	0·26	0·19	0·19	0·11	0·20	0·03	0·19	0·25	-

Table 4. A summary of M separability statistics from 55 paired comparisons between all 11 forest types (8 primary types, Ra, Re and Rg) and each spectral band and vegetation index. The corrected Landsat TM image is compared with the filtered image showing 33% overall increase in average M values for filtered spectral bands and vegetation indices. Percent increase is calculated as %Inc = (*nf* – *f*)*100 where *nf* = the non-filtered TM image and *f* = the filtered TM image.

	nf	***f***		***nf***	***f***		***nf***	***f***	
TM band	**Ave M**	**Ave M**	**%Inc**	**Ave M≥1**	**Ave M≥1**	**%Inc**	**Total # M≥1**	**Total # M≥1**	**Diff**
1	0.96	1.66	*42*	1.68	2.76	*39*	23	28	*5*
2	0.83	1.21	*31*	1.47	1.93	*24*	22	29	*8*
3	0.91	1.38	*34*	1.67	2.53	*34*	23	26	*9*
4	0.38	0.55	*31*	1.05	1.08	*3*	3	9	*3*
5	0.45	0.66	*32*	1.14	1.32	*14*	3	13	*5*
7	0.36	0.56	*36*	1.00	1.44	*31*	3	6	*3*
		Ave	***34%***		***Ave***	***24%***		***Ave***	**6**
Veg Index									
ND53	0.93	1.51	*39*	1.42	2.17	*34*	26	31	*5*
WDRVI	0.90	1.44	*38*	1.62	2.21	*26*	21	29	*7*
NDVI	0.87	1.43	*37*	1.61	2.30	*30*	21	30	*3*
EVI	0.33	0.45	*26*	1.02	1.04	*2*	3	6	*6*
MSARVI	0.31	0.44	*30*	1.05	1.17	*11*	1	6	*10*
SARVI	0.27	0.37	*27*	1.07	1.13	*6*	1	4	*3*
		Ave	***33%***		***Ave***	***22%***		***Ave***	**6**

Table 5. Results from spectral separability comparisons among 11 forest types using spectral reflectance and NDVI. Shaded areas are comparisons that resulted in what are considered well separated or significantly different forest types. Each of the 3 tables compares forest types by; a) M values using NDVI as a single index, b) JM distances values using a 7 band image, and c) MRPP significance tests using a Euclidean distance matrix from 7 bands.

a

Type	Pc	Pp	Qp	Pd	Ma	Cy	Ta	Va	Ra	Re	Rg
Pc	-										
Pp	0·2	-									
Qp	0·5	0·5	-								
Pd	0·5	0·4	0·1	-							
Ma	1·2	2	2·6	2·6	-						
Cy	1·7	2·9	3·8	4	0·3	-					
Ta	1	1·6	2·1	2·1	0·3	0·7	-				
Va	1·2	2	2.7	2.7	0·2	0·5	0·2	-			
Ra	1	1.2	0·7	0·9	3·6	5·4	3	3·7	-		
Re	1	0·1	0·4	0·4	1·3	1·7	1	1·3	0·9	-	
Rg	0·9	0·1	0·7	0·8	2	2·5	1.8	2·1	0·4	0·8	-

b

Type	Pc	Pp	Qp	Pd	Ma	Cy	Ta	Va	Ra	Re	Rg
Pc	-										
Pp	0·79	-									
Qp	1·73	1·4	-								
Pd	1·3	1	0·91	-							
Ma	1·82	1·93	2	2	-						
Cy	1·99	2	2	2	1·72	-					
Ta	1·64	1·76	2	1·98	0·58	1·83	-				
Va	1·77	1·95	2	2	0·85	1·56	0.9	-			
Ra	1·96	1·88	1·48	1·61	2	2	2	2	-		
Re	1·72	1·53	1·71	1·78	1·99	2	1·91	1·99	1·92	-	
Rg	1·7	1·54	1·67	1·72	1·99	2	1·95	1·99	1·86	1·49	-

c

Type	Pc	Pp	Qp	Pd	Ma	Cy	Ta	Va	Ra	Re	Rg
Pc	-										
Pp	0·24	-									
Qp	**	**	-								
Pd	0·16	0·18	0·12	-							
Ma	**	**	**	*	-						
Cy	0·004	0.002	*	0.006	0·68	-					
Ta	*	**	**	0.004	0·08	0·32	-				
Va	**	**	**	*	0·11	0·63	0·11	-			
Ra	**	**	0·01	*	**	*	**	**	-		
Re	**	**	**	**	**	**	**	**	**	-	
Rg	**	**	**	**	**	**	**	**	**	*	-

*significant at α = 0·05 (Bonferroni corrected = 0·0009)

**significant at α = 0·01 (Bonferroni corrected = 0·00018)

Table 6. Error matrices comparing pixels classified using MLA with validation pixels. Comparisons are expressed as a percent of correctly classified pixels in bold type along the main diagonal of the matrix. Producers and uses accuracy represent the level of accuracy for each individual forest type. Comparisons are made in a hierarchical fashion from a) 11 forest types, b) 8 forest types, and c) 7 forest types combining confused classes based on group membership from hierarchical cluster analysis.

a

Validation pixels

Type	Pc	Pp	Qp	Pd	Ma	Cy	Ta	Va	Ra	Re	Rg	Prod. Acc.	User Acc.
Pc	**42**	23	0	2	0	0	1	0	0	3	2	42	53
Pp	18	**25**	6	3	0	0	1	0	0	2	6	25	47
Qp	2	2	**79**	24	0	0	0	0	5	4	7	79	65
Pd	29	30	12	**70**	0	0	0	0	6	0	4	70	27
Ma	0	3	0	0	**47**	10	27	6	0	0	0	47	43
Cy	0	0	0	0	0	**67**	2	10	0	0	0	67	90
Ta	0	10	0	0	25	0	**46**	2	0	3	0	46	43
Va	5	4	0	0	25	23	23	**82**	0	2	1	82	44
Ra	0	1	2	1	0	0	0	0	**87**	0	0	87	97
Re	3	0	1	0	0	0	0	0	0	**72**	6	72	90
Rg	1	1	0	1	2	0	0	0	2	13	**72**	72	78

Overall Accuracy = (4379/6921) 63·3%

Kappa Coefficient = 0·59

b

Validation pixels

Type	Pm	Qp	Ma	Cy	Ta	Ra	Re	Rg	Prod. Acc.	User Acc.
Pm	**85**	19	0	0	1	6	5	13	85	82
Qp	6	**79**	0	0	0	5	4	7	79	65
Ma	1	0	**47**	10	16	0	0	0	47	45
Cy	0	0	0	**67**	6	0	0	0	67	90
Ta	5	0	50	23	**77**	0	5	1	77	55
Ra	1	2	0	0	0	**87**	0	0	87	97
Re	1	1	0	0	0	0	**72**	6	72	90
Rg	1	0	2	0	0	2	13	**72**	72	78

Overall Accuracy = (5245/6804) 77·3%

Kappa Coefficient = 0·73

C Validation pixels

Type	Pm	Qp	Cy	Ta	Ra	Re	Rg	Prod. Acc.	User Acc.
Pm	**86**	19	0	1	6	5	13	86	82
Qp	6	**79**	0	0	5	4	7	79	65
Cy	0	0	**74**	7	0	0	0	74	90
Ta	5	0	26	**91**	0	5	1	91	66
Ra	1	2	0	0	**87**	0	0	87	97
Re	1	1	0	0	0	**72**	6	72	90
Rg	1	0	0	0	2	13	**72**	72	78

Overall Accuracy = (5090/6284) 81·0%

Kappa Coefficient = 0·77

Figures

Fig. 1. Map of the San Juan-La Selva Biological Corridor study area, 1997 forest cover and the location of all primary forest plots. Plots that appear in Nicaragua are *Raphia* palm swamps along the San Juan River referenced to the TM image using aerial photo interpretation.

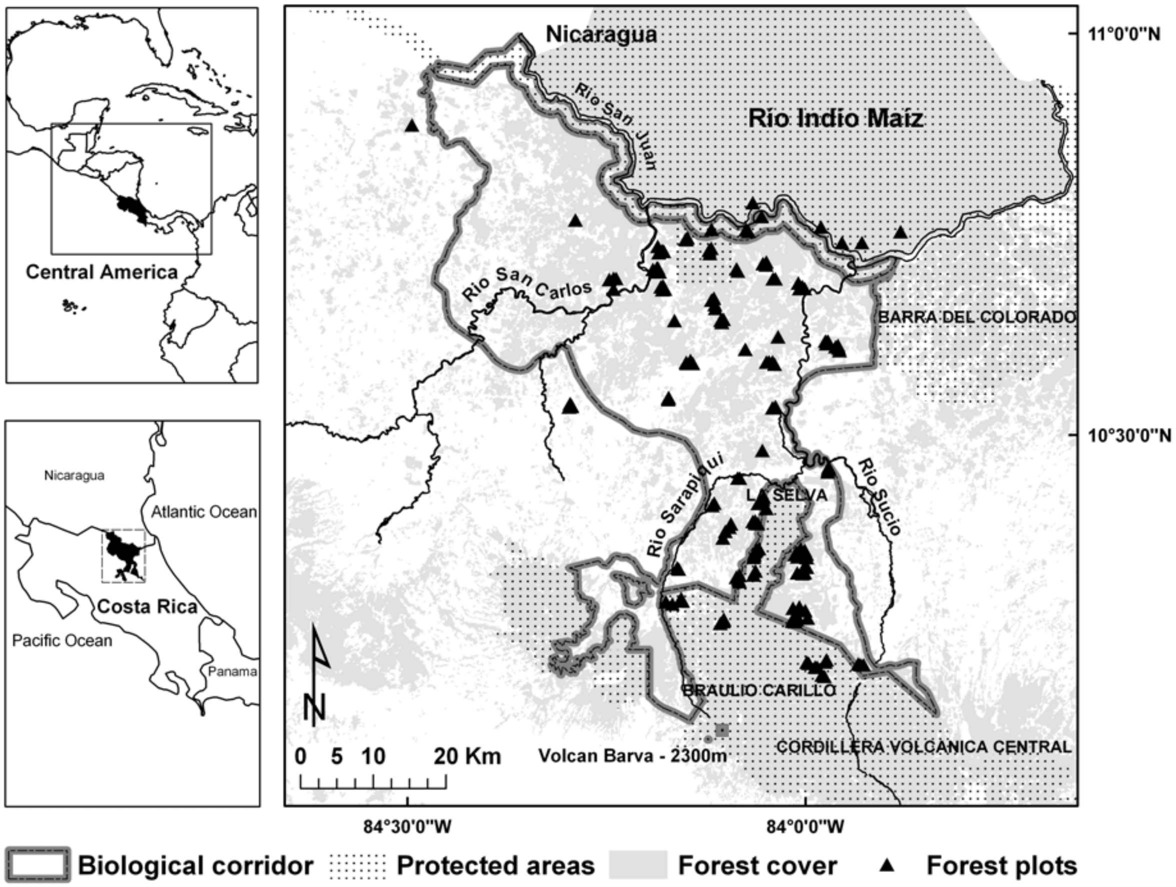


Fig. 2. Elevation ranges for georeferenced forest plots and derived forest types including *Raphia* palm swamps. Reforestation and forest re-growth are not included as these occurred throughout the study area.

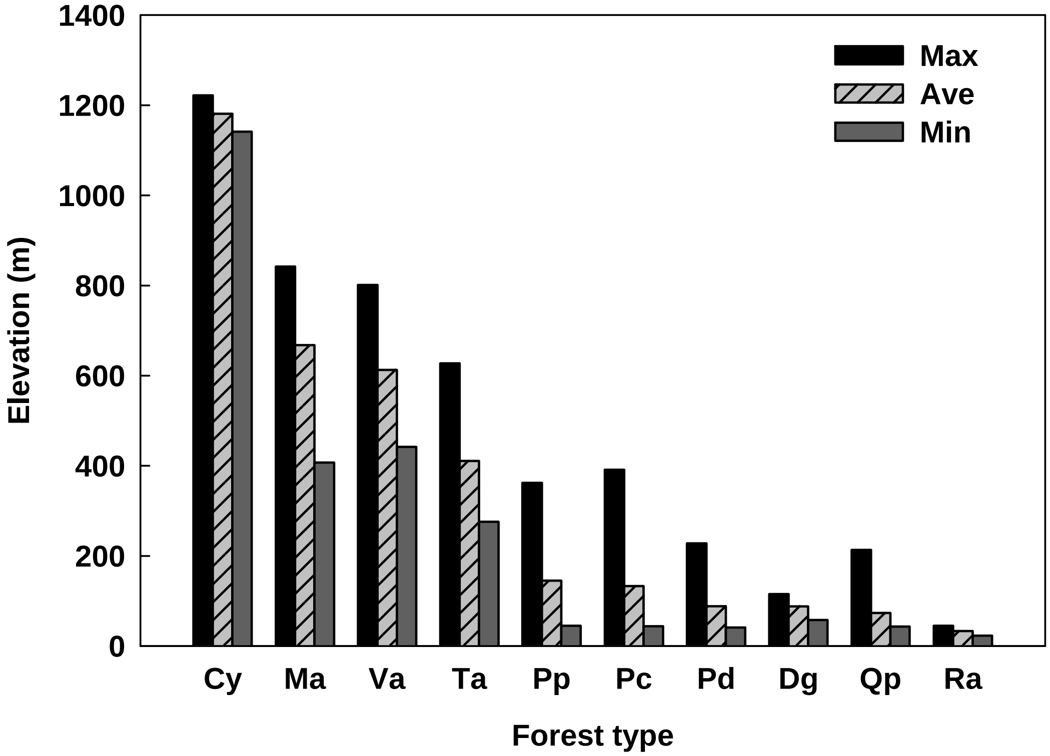


Fig. 3. NMS ordinations of forest plots and trees species overlain with forest types using, a) ordination axes 1 and 2 and b) ordination axes 1 and 3. Axes are scaled proportionally to the longest axis as a percent to accurately represent similarity relationships among plots and forest types. Axis 1 shows a strong elevation gradient with concomitant changes in forest composition. Axis 2 indicates a precipitation gradient primarily for the lowland forest types with increased seasonality towards zero. Axis 3 was difficult to interpret, but corresponds to plots and tree species differences from the Dg forest type in the western most part of the corridor.

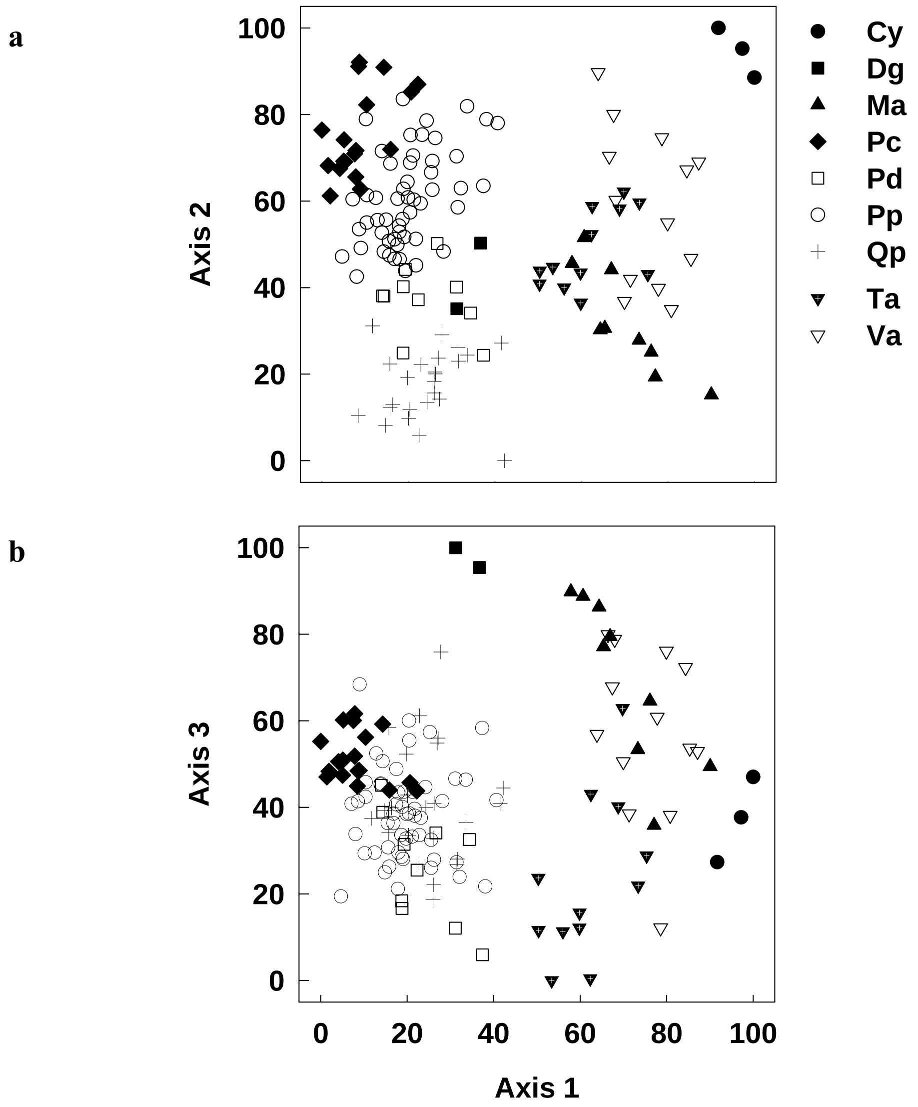


Fig. 4. Mantel Correlogram indicating the level of spatial autocorrelation for tree species and measured environmental gradients (Elevation, total annual precipitation and average monthly temperature) among all 144 forest plots grouped by 22 distance classes. Points above or below the dotted horizontal lines indicate significant positive or negative autocorrelation at each distance interval.

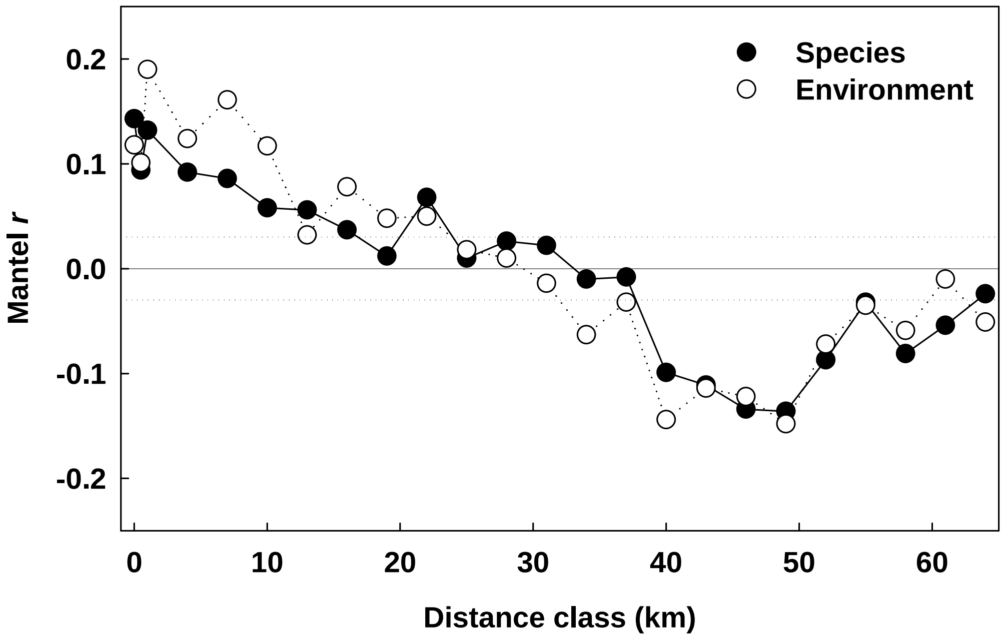
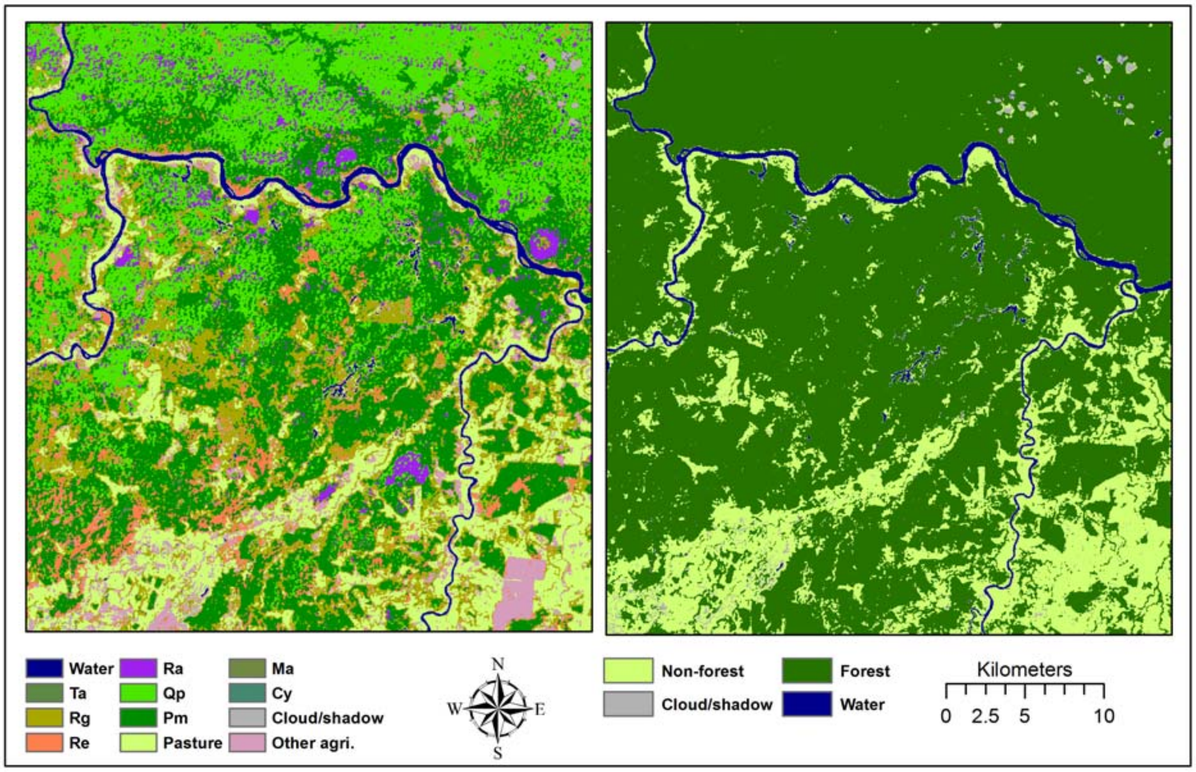


Fig. 5. Forest types mapped for a portion of the SJLS Corridor in the lowlands bordering with Rio San Juan and Southern Nicaraguan forests. Forest types that were identified from cluster analysis are mapped at the 77% overall accuracy level as compared to a "forest/non-forest" level of classification from the 2001 TM image.



Chapter 2
Landscape-scale Environmental and Floristic Variation in Costa Rican Old-growth Rain Forest Remnants

ABSTRACT

Studies of tropical rain forest beta-diversity debate environmental determinism versus seed dispersal limitation as principal mechanisms underlying floristic variation. Central American studies lack soil chemical and physical data matched with landscape-scale vegetation measurements. We examined the relationship between soil characteristics, terrain and climate variation with rain forest composition for a 3000 km^2 area in northeastern Costa Rica. Canopy tree and palm species abundance and soils were measured from 127, 0.25-ha plots across Caribbean lowlands and foothills. Plot elevation, slope, and temperature and precipitation variation were taken from digital grids.

Ordination of forest data yielded three floristic groups with strong affinities to either foothills or lowland environments. Variation in floristics, soil texture and climate conditions measured from distance matrices showed parallel patterns of significantly positive spatial autocorrelation up to 13 km and significantly negative correlation after 40 km. Partial Mantel tests showed significant correlations between floristic distance and terrain, climate and soil textural variables controlling the effect of geographical distance. Separate comparisons for palm species showed significant correlation with Mg and Ca concentrations among other soil factors. Palms demonstrated a stronger relationship with soil factors than did canopy trees. Correlation between floristic data and geographical distance, related to seed dispersal or unmeasured variables, was not significant when controlling for statistically significant soil characteristics and elevation. Canopy trees and palms showed differing relationships to soil and other environmental factors, but lend greater support for a niche-assembly hypothesis than to a major role for dispersal limitation in determining species turnover for this landscape.

INTRODUCTION

DETERMINING FACTORS THAT DRIVE RAIN FOREST BETA-DIVERSITY is fundamental to characterizing the floristic composition of neotropical landscapes. Rapid deforestation since the 1950s has left dispersed forest fragments over much of Central and South America that are important to maintaining regional floristic diversity (Defries *et al.*

2005, Mayaux *et al*. 2005). Beta-diversity, defined here as spatial turnover in species composition (Condit *et al*. 2002), is well integrated into temperate zone biodiversity assessment (Scott *et al*. 1998), but has yet to play a prominent role in conservation planning for tropical areas. Floristic variation with respect to environmental differences and geographical location is poorly quantified for wet tropical areas given logistical constraints and challenging taxonomy (Ruokolainen *et al*. 1997). As a result, differences in rain forest composition are broadly characterized by relatively few forest types with wide reaching implications for biodiversity conservation (Tuomisto *et al*. 2003a).

Distinctive floras on poor fertility or inundated sites are well acknowledged aspects of rain forest beta-diversity (ter Steege *et al*. 1993, Tuomisto *et al*. 1995, Duivenvoorden 1995, Duque *et al*. 2002). Recent quantitative assessments of Panamanian and Amazonian forest plots provide evidence that forest composition on *tierra firme* sites (e.g., non-flooded or less extreme edaphic environments) varies with greater consistency than previously considered (Condit *et al*. 2002, Phillips *et al*. 2003, Tuomisto *et al.* 2003a, b, Chust *et al.* 2006). However, factors accounting for floristic variation contrast between geographical location, scale of analysis and plant groups investigated (Ruokolianen *et al*. 2002, Phillips *et al*. 2003). For example, Condit *et al*. (2002) found that tree species similarity for Panamanian forest plots was as low as 1% at 50 km distance, but showed consistent similarities of 30 to 40% up to 100 km apart for Amazonian plots.

Contemporary points of view distinguish between niche and dispersal assembly as principal mechanisms for variation in rain forest composition (Hubbell 2001, Jones *et al.* 2006). From as early as Gleason (1927) and Whittaker (1967), Niche theory posits that plant species show non-random distributions that vary according to environmental conditions or gradients. Environmental determinism and competitive interaction are assumed to mediate plant community organization and are frequently the basis for models of floristic patterns (Franklin 1995, Austin 2002). A growing number of tropical studies reveal that soil, climate and topographic differences are significantly related to rain forest tree, fern and palm species distributions at local (< 1 km^2) (Ruokolainen & Tuomisto 1997, Vormisto *et al.* 2004, Poulsen *et al*. 2006), meso- (1 – 100 km^2) (Clark *et al*. 1995, Clark *et al*. 1999, Jones *et al*. 2006) and landscape-scales (100 – 10,000 km^2) (Tuomisto *et al*. 1995, Pyke *et al*. 2001, Tuomisto *et al.* 2003a, b, c, Phillips *et al*. 2003).

In contrast, dispersal assembly challenges whether environmental factors are principal drivers of the present variation in old-growth rain forest composition (Hubbell *et al*. 1999, Hubbell 2001, Condit *et al*. 2002, Chust *et al*. 2006). Hubbell *et al*. (1999) noted that small-scale disturbance accommodates opportunistic establishment by individuals from the surrounding meta-community, rather than by species with a competitive advantage. In the event that disturbances, common to neotropical rain forest (Hartshorn 1980, Hubbell *et al*. 1999), and seed dispersal are highly random occurrences, tree species similarity is expected to decline logarithmically with increasing geographical distance (Hubbell 2001, Condit *et al*. 2002). Thus, an alternative hypothesis is that distance dependant processes significantly influence forest composition, above that from environmental factors.

Chust *et al*. (2006) conclude that geographical distance was a stronger predictor of tree species composition than precipitation or elevation variables from plots across the Panama Canal Watershed, consistent with a dispersal limitation hypothesis. No data were available to assess soil differences related to forest composition, however, as noted by the authors (Chust *et al*. 2006). Soil nutrient status and physical prosperities have shown significant correlation with tree, palm and fern species on rain forest plots at multiple spatial scales (Duque *et al*. 2002, Phillips *et al*. 2003, Jones *et al*. 2006, Poulson *et al*. 2006). Moreover, environmental factors can show strong covariance patterns with vegetation at increasingly distant sample locations (Legendre & Fortin 1989). In the case where multiple factors are correlated with floristic composition, spatial autocorrelation among variables can add greater importance to observed relationships than is actually warranted (Wagner & Fortin, 2005).

The present study evaluates relationships between rain forest composition and environmental factors on *tierra firme* sites in northern Costa Rica. We sought to clarify quantitative relationships between forest composition, soil and climate factors for a 3,000 km^2 Caribbean forest landscape accounting for the effect of spatial autocorrelation. Our objectives were to, 1) quantify floristic and environmental differences among old-growth forest remnants at a landscape-scale, 2) assess the degree of spatial autocorrelation for floristic data and environmental variables at increasingly distant sample locations and 3) test for significant relationships between niche and geographical distance related factors potentially linked to rain forest beta-diversity. A total of 127, 0.25-ha forest plots were established to measure floristic composition of remnant old-growth forest. Mid- to upper-canopy trees and aborescent palms (family Arecaceae) were the principle focus of data collection and analyses. The logarithm of geographical distance from spatially referenced plot locations was used to approximate seed dispersal and distance related processes following Hubbell (2001). Statistical comparisons with trees and palms together and palms separately were evaluated to distinguish among different plant groups occupying forest canopies. Several studies suggest that spatial variation differ among plant groups (e.g., tree and palm species) and environmental factors evaluated (ter Steege *et al*. 1993, Vormisto *et al*. 2004, Jones *et al*. 2006, Poulsen *et al*. 2006).

METHODS

FIELD MEASUREMENTS. – Forest and soil measurements were taken from old-growth forest remnants across northeastern Costa Rica (Fig. 1). A majority of the plots were located in the San Juan – La Selva Biological Corridor that is one the largest forest aggregations remaining outside national parks in Costa Rica (Watson *et al*. 1998). Human settlement in the area since the 1950s has reduced forest cover to dispersed remnant patches situated between pasture and croplands (Butterfield 1994).

The physical environment is influenced by elevation that ranges from sea level to above 3000 m in the Central Volcanic Range (Lieberman *et al.* 1996). Monthly temperature averages near 24 °C in the lowlands, but decreases to as low as 10°C at the highest elevations (Lieberman *et al*. 1996). Annual precipitation ranges from 4,500 mm at mid-elevations in the study area (Hartshorn & Peralta 1988, Grieve *et al*. 1990) to 3,000 mm in western lowland sites according to WorldClim precipitation grids described below (Fig. 1). Eastern lowlands and the foothills have consistently high monthly rainfall ≥150 mm throughout the year. Lower precipitation occurs during the month of March in western lowlands with average monthly rainfall <100 mm (Fig. 1). Lowland terrain is a mixture of steep hills, alluvial terraces, and swamplands interrupted by hills reaching 400m elevation (Fig. 1). Soils are mainly Pleistocene aged Ultisols derived from andesitic parent material with evidence of ash falls above 500 m elevation (Grieve *et al*. 1990, Sollins *et al*. 1994) and Inceptisols derived from alluvial and colluvial deposits overlaying old lava flows (Harshorn & Peralta 1988, Sollins *et al*. 1994).

A total of 127, 0.25-ha plots (50 x 50 m) were established between 40 m to 1200 m elevation across the environmental and geographical gradients described above avoiding extreme site conditions (*e.g.*, palm and forested swamps) (Fig. 1). A minimum of two plots were located in forest remnants that range in size from 40 ha to more contiguous forest patches >1,000 ha. Plots were positioned at random following a compass line for a minimum distance of 150 m from a forest edge and at least 300 m from another plot. Areas with intensive tree harvest, wind or other evidence of recent disturbance were avoided during sampling. Inter-plot distances ranged from 0.3 to 61 km. On each plot, a stem diameter at breast height (d.b.h. = 1.37 m) and species name was recorded for all trees ≥ 30 cm d.b.h and arborescent palms and ferns (family Cyatheaceae) ≥ 10 cm d.b.h. Diameters were taken immediately above the bole swelling for buttressed trees. All plots were georeferenced from a canopy gap with a global positioning system with an estimated horizontal error of ~12 m.

To assess soil conditions, a 40-cm soil sample was collected from plot center using a 7-cm diameter dutch-type auger. Soil depth and presence of a high water table were determined with a 1.5-m metal probe, though forest measurements were not taken on sites with evidence of consistently saturated soil (e.g., water present or strong gleying). Organic material was cleared from the top 1 to 2 cm of each site prior to collecting a soil sample. Soil was placed in a labeled plastic bag and transported to the soils laboratory at the Centro Agronómico Tropical de Investigación y Ensenañza (CATIE) in Turrialba, Costa Rica. Each sample was air dried in a screened drying room before laboratory analysis.

Soil chemical and physical properties from were determined with the following procedures. Soil pH in water was measured and extractable K and P were measured using Modified Olsen extractions with a 0.5 M sodium bicarbonate ($NaHCO_3$) solution at a pH of 8.5 (Olsen and Sommers 1982). Extractable Ca, Mg and total acidity extractions were done in a 1N suspension of potassium chloride (KCl) using methods documented by Diaz Romeu and Hunter (1978). Percent soil organic matter (OM) was measured using the total combustion method following Nelson and Sommer (1996) with pre-treatment to eliminate carbonates. Soil texture (percent sand, silt and clay) was determined by the Bouyoucos method (Bouyoucos 1936). Textural classes were assigned following methods from the USDA Soil Survey Staff (1975). Selected soil properties were those likely to affect plant growth and rain forest composition (Sollins 1998). Total acidity was used as an indicator of potential aluminum (Al) toxicity and soil textural features as indicators of drainage and water retention (Sollins *et al*. 1994, Sollins 1998).

Climate and terrain variables for georeferenced plots were taken from digital data layers in a geographic information system (GIS). Plot elevations were taken from a 90-m digital elevation model (DEM) obtained from the U.S. Geological Survey Shuttle Radar and Topography Mission (SRTM) dataset (http://edc.usgs.gov/products/elevation.html). Percent slope was estimated from the DEM using the Spatial Analyst extension in ArcMap v. 9.1 (ESRI 2005). Average annual temperature and precipitation values for plot locations were taken from WorldClim 30 arc-second grids (~1-km resolution) for comparisons with forest composition (Fig. 1). The WorldClim "bioclimatic" data set is designed for niche modeling of plant and animal species (http://www.worldclim.org/). Digital surfaces of annual and seasonal climate cycles are derived from weather station records of monthly temperature and precipitation, latitude, longitude and SRTM elevation data. A description of interpolation methods and accuracy is found in Hijmans *et al*. (2005).

Coefficients of variation (CV) and minimum monthly precipitation values were used as indices of rainfall seasonality for statistical comparison with floristic data. Metrics of seasonal temperature variations used were minimum monthly temperature (e.g., coldest month temperature) and monthly temperature standard deviation x 100 as indices of temperature seasonality potentially important to rain forest composition at this scale (Pyke *et al*. 2001).

STATISTICAL ANALYSES. – Modified t-tests and Pearson's correlations (Pearson's *r*) were used to determine significant relationships ($P < 0.05$) between soil, climate and terrain variables (*e.g.*, elevation and slope). Modified t-tests perform comparisons accounting for spatial autocorrelation among variables by limiting the effective sample size and using corrected degrees of freedom to assess significance following Dutilleul *et al*. (1993).

Statistical comparisons between forest composition and environmental factors were made using distance matrices. Separate Sorensen (Bray-Curtis) distance (dissimilarity) matrices were computed for abundance data using tree and palm species combined and palm species separately for comparisons with environmental and geographical distances. A distance matrix from palm species included 117 plots that contain at least one individual of the four most abundant palm species (*Iriartea deltoidea*, *Euterpe precatoria*, *Socratea* *exorrhiza*, and *Welfia regia*). Soil and environmental variables were log-transformed and a separate Euclidean distance matrix was derived for each variable. Plot coordinates were used to generate geographical distance among plots that was log-transformed to approximate the effect of random species dispersal (Hubbell 2001). Hierarchical cluster analysis using the Flexible beta linkage method (beta = -0.25) and Nonmetric Multidimensional Scaling (NMS) were used to characterize floristic composition for plots distributed across a range of conditions and geographical locations. A total of 20 runs with real data and 50 runs with randomized data were used to evaluate the stability of the final ordination. Density-diversity curves were used to determine species abundance patterns between floristic groups (Whittaker 1965). The PC-ORD statistics package v. 5.01 was used for these analyses (McCune & Medford 1999). Pearson correlation coefficients between individual species, environmental factors geographical distance (e.g., X and Y coordinates) and ordination axes were used to aid interpretation of NMS results.

Mantel correlation comparisons (Mantel's r) between matrices were performed using the PASSAGE statistics package v. 1.1 (Rosenburg 2001). The standardized Mantel statistic is similar to a Pearson product-moment coefficient, but is calculated comparing paired distance matrices rather than original variables (Legendre & Fortin 1989). The degree of spatial autocorrelation between floristic composition, environmental variables and geographical distance was first evaluated via Mantel Corrrleograms (Legendre & Fortin 1989). Mantel coefficients were compared at distance classes from 0 - 0.5 km to 58 - 61 km used to observe the spatial autocorrelation relationships among variables across a range of inter-plot distances. Classes were closely spaced initially starting from an inter-plot distance of 500 m and were then set at regular 3-km increments.

Partial Mantel tests were used to determine the relationship between two distance matrices controlling the effects of a third factor (e.g., environmental or geographical distance). Species and environmental distances were compared controlling for geographic distance. Geographical distance itself was considered an important variable related to the dispersal assembly hypothesis (Condit *et al.* 2002, Chust *et al.* 2006) and compared with floristic distances controlling for environmental factors. Statistical significance was tested for each comparison using Monte Carlo permutations implementing 999 matrix randomizations ($\alpha < 0.05$).

RESULTS

SOIL AND TERRAIN CONDITIONS. - Soils showed a wide range of chemical and physical properties along the gradients sampled (*e.g.*, geographical, elevation and climate) (Table 1). Cation concentrations (Ca, K, Mg), pH and extractable P showed a wide range of values, but relatively low standard deviation. A total of six plots measured at low elevation sites with greater cation concentrations contributed to the range observed. Extractable phosphorous (P) was also highest for these plots. Forest soils sampled were most commonly acidic (pH 4.57 ± 0.38) and low in bases (Table 1). Significantly positive Pearson correlations between pH and cation concentrations, and P, to a lesser degree, indicated a relationship between acidity and native soil fertility (Table 2). Total acidity was significantly and negatively correlated with elevation and Mg concentrations, but had low standard deviation across sites (Tables 1, 2). No significant trend between cations and terrain variables (e.g., elevation and percent slope) was observed (Table 2).

Soil physical properties showed the most substantial differences across the study area (Table 1). A high range in silt content (7 – 42%) and low standard deviation (± 5.6) was attributed to four plots across a single large forest remnant in the lowlands on flat terrain with silty-clay textures that was potentially affected by seasonal flooding. These plots were also high in cation and P concentrations. Soil clay, sand and organic content differed considerably across the study landscape and were highly and significantly correlated with elevation (Table 2). Soils sampled in the foothills of the Central Volcanic Range were clearly higher in sand and organic material contrasting with clay-rich soils in the lowlands. Percent slope showed negative and positive correlation with clay and sand content respectively, but were not significant from Modified t-tests (Table 2).

CLIMATE AND TERRAIN CONDITIONS. - Temperature and precipitation patterns showed notable differences between plots, but did not cross extreme climatic gradients (e.g., wet to dry tropical environments) (Table 3). The largest coefficients of variation for monthly precipitation were approximately half of what is found in dry tropical forest environments (data not shown) recognized by the Holdridge Life Zone system (Holdridge 1967). Mean temperatures were moderately cooler for plots in the foothills (minimum monthly temperature of 15 °C) with moderate seasonal differences in the lowlands (Fig. 1). Seasonally lower precipitation was observed for plots in the western lowlands although annual precipitation was generally high across all plots (Fig. 1, Table 3). Weather station records obtained for the study area roughly confirm temperature and precipitation variation observed in the lowlands (Sesnie, unpublished data). A drier period above 1000 m elevation (Fig. 1) could not be confirmed as weather stations are sparsely distributed in this area however a declined in annual rainfall at 1800 m is noted in Hartshorn and Peralta (1988) for this area.

The elevation range of plots (41 – 1222 m) was the most important source of variation in terrain and showed a strong negative correlation with temperature seasonality (Pearson $r = -0.64$, $P < 0.001$) and minimum monthly temperature (Pearson $r = -0.98$, $P < 0.001$). No other climate variables were correlated with elevation or slope from Modified t-tests (data not shown). Precipitation variation between plots in the lowlands and foothills did not show strong covariance patterns with elevation. Complex rainfall patterns that vary with distance from the Caribbean coast and elevation changes likely confound correlation with elevational differences.

FLORISTIC VARIATION AND MEASURED GRADIENTS. - A total of 189 species with >1 individual encountered on all plots (5,066 individuals) were used for statistical analyses. A total of 90 % of the individuals used for analysis were identified to the species level by field taxonomists or sample material taken to National Institute for Biodiversity (INBio) Herbarium in San José, Costa Rica for identification by Nelson Zamora. All others were identified to genus and given a species number that was repeated for individuals with similar morphological characteristics. Tree species accounted for 61 % of the individuals sampled and 38 % were four of the most abundant palm species (*I. deltoidea*, *E. precatoria*, *S. exorrhiza*, and *W. regia*). Arborescent ferns ≥10 cm d.b.h (*Cyathea spp.*) and other palms (*Bactris spp.*) were measured on plots, but accounted for < 1 % of individuals and were not used for separate comparisons. Fewer plots at the highest elevations where arborescent ferns are more common (Harshorn & Peralta 1988, Lieberman *et al.* 1996) account for the low number of individuals recorded in comparison to palms.

To observe floristic variation among plots, three principle floristic groups resulting from a hierarchical cluster analysis of plots were overlaid on NMS ordinations (Fig. 2). A three dimensional solution was obtained from ordinations with a final stress index of 16.7 that was significantly better than if by chance ($P < 0.05$) from Monte Carlo randomizations for 1 to 6 dimensions tested. The amount of variance explained was 22, 30 and 30 % for axis 1, 2 and 3 respectively (82 % total). Floristic groups were generally termed foothills, *Pentaclethra macroloba* and *Qualea paraensis* forest in reference to distinctive features of each group. Species richness for the floristic groups is substantially higher than indicated by the individual species referenced.

Plots along axes 2 and 3 divide forest into floristic groups with an affinity toward the foothills (n = 31 plots) or the lowlands (Fig. 2). Lowland sites were dominated by *P. macroloba* (n = 61 plots) showing a strong negative correlation with axis 3 (Fig. 2). Composition differences between the two lowland floristic groups were determined by an increased abundance for trees in the Vochysiaceae family (e.g., *Q. paraensis, Vochysia allenii, Vochysia ferruginea*) positively correlated with axis 3 and abundant palm species negatively correlated with axis 2 (n = 29 plots) (Fig. 2). Dominance-diversity curves indicate lower abundance of common canopy species for foothills and *Q. paraensis* forest compared with *P. macroloba* forest (Fig. 3). Twice the amount of area sampled in forest characterized by *P. macroloba* helps explain a greater total number of species encountered for this floristic group (Fig. 3).

Environmental variables demonstrating strong positive or negative correlation (Pearson's *r*) with ordination axes are given in order of importance. Floristic differences between the foothills and lowlands along axis 3 were positively correlated with sand content (Pearson $r = 0.65$), and plot elevation (Pearson $r = 0.69$) and negatively correlated with all temperature variables (Pearson $r \geq -0.70$) (Fig. 2). Clay content was negatively correlated with axis 3 (Pearson $r = -0.63$) in the direction of *P. macroloba* dominated forest at the lower end of this axis. Axis 2 showed positive correlation with elevation (Pearson $r = 0.40$) and a negative correlation with soil texture using a ratio of clay to sand (Pearson $r = -0.42$). Axis 2 also showed a strong negative correlation with geographical distance (Pearson $r = -0.61$) in a south to north direction from Y of plot coordinates X and Y. Modified t-tests indicate that a number of the factors correlated with ordination axes are inter-correlated with each other (Table 2). Axis 1 was negatively correlated with total annual precipitation (Pearson $r = -0.71$) and minimum monthly precipitation (Pearson $r = -0.64$), but was less interpretable with a lower proportion of the total variance explained for this axis. Other environmental factors showed weaker correlation with ordination axes.

SPATIAL AUTOCORRELATION AMONG VARIABLES. – Multivariate Mantel Correlograms demonstrate that forest composition is likely to be similar for plots spaced at shorter distances, which are more likely to occupy comparable environments (Fig. 4a, b). Floristic and environmental variables were significantly autocorrelated up to the 10 - 13 km class (Fig. 4a, b). A decline in floristic similarity with geographical distance, determined by Mantel *r*, was steeper up to the 4 – 7 km class in parallel with elevation and climate distances (Fig. 4a). Soil physical properties, sand and clay, were significantly correlated with geographical distance up to the 22 – 25 km class (Fig. 4b). An increased positive spatial autocorrelation in floristic composition at the 22 – 25 km distance class was related to plot pairs from the foothills and in similar lowland environments (*cerros* or hills) at this distance (Fig. 1, 4). Significantly negative spatial autocorrelation for floristic distance after 40 km showed a pattern consistent with environmental distances that were evident for most geographic distance classes (Fig. 4a, b). Significant negative correlations indicate that there are few or no species in common on plots > 40 km distance which also occupy differing environmental conditions.

MANTEL COMPARISONS OF FLORISTIC, ENVIRONMENTAL AND GEOGRAPHICAL VARIABLES. – Comparisons above provided a basis for testing the null hypothesis of no relationship between floristic and environmental distances once accounting for spatial autocorrelation (geographical distance). Alternatively, geographical distance is significant factor correlated with floristic variation among plots once controlling the effect of significant environmental factors.

Simple Mantel tests comparing a matrix of trees and palms combined and soil factors resulted in significant correlations for sand, clay and organic matter (Table 4). Partial Mantel tests showed no loss of significance after controlling for the effect of geographical distance. Similar trends were observed with the separate matrix for palm species although silt content was also a significant factor (Table 4). Box plots for soil texture and each floristic type from ordination show high contrast between foothills and lowland floristic groups (Fig. 5). Foothills forest is characterized by high sand content and organic matter in contrast to lowland forest on clay soils. Distributions for sand and clay were similar for the two lowland groups, but with less varied soil textures for *P. macroloba* dominated forest (Fig. 5).

From here, we limit presentation of results to Partial Mantel tests unless a loss of significance was observed. No significant relationships were found with soil chemical properties for canopy tree and palm species combined (Table 4). Results likely reflect the influence of canopy trees that are not sensitive to low deviations in the chemical properties observed. Conversely, comparisons with a matrix of the four most abundant palm species showed significant relationships with differences in Ca and Mg concentrations (Table 4). Soil pH and total acidity and were also significantly related to palm distributions that are significantly correlated with other soil chemical properties (Table 2). Silt was weak, but significantly correlated with palm distances likely due to a few soil samples showing strong differences in silt content.

Terrain variables elevation and slope were also significant factors for trees and palms combined, but slope was not a strong variable (Table 4). These results were not surprising as elevation covaries with significant soil physical properties (Table 2) and other important climate variables. Slope was a weak, but significant variable likely due to the scale of the elevation data (90-m) used and limitations for estimating local hill-slope variation. Palm species were not significantly related to percent slope from separate comparisons sharing this same limitation. Plots (50 m x 50 m) were generally located at a single slope position however hilly terrain in the foothills changes both horizontal and vertical to the slope and can vary at distances shorter than 50 m in this landscape.

Climate variables all showed a significant relationship with combined floristic data with moderate differences in seasonal and annual precipitation and temperature variables (Table 3). Precipitation seasonality and minimum month precipitation were not significantly correlated with palms separately controlling for geographical distance. No large turnover in palm species composition was observed on plots in the lowlands. Significant correlation between palm species and temperature variables were likely linked to fewer palm species present in foothills environments with cooler temperatures. An exception was the most wide spread palm species, *I. deltoidea,* that showed relatively high abundances in the foothills though all species of arborescent palms were absent from plots above 1000 m.

Geographical distance was significantly related to floristic distance at the $P < 0.001$ level from simple Mantel comparisons with floristic data (Table 4). Geographical distance remained a significant factor controlling for elevation, but showed a loss of significance ($P >$

0.05) when the effect of elevation and soil physical properties (*e.g.*, clay or sand content) were controlled (Table 4). Elevation was the strongest factor related to floristic composition (*e.g.*, trees and palms) followed by clay content. Separate comparisons with palm species resulted in significant correlations with geographical distance controlling for elevation and clay, but showed a loss of significance incorporating a matrix from Mg and elevation combined (Table 4). Mg concentrations were highly and significantly correlated with other soil cations, pH and total acidity, to a lesser degree (Table 2). Elevation is also well correlated with soil physical properties indicating important relationships among environmental variables significantly related to palm species distributions. Geographical distance was a less important variable once controlling for factors related to multiple environmental gradients.

DISCUSSION

Variation in forest composition along environmental gradients for this area has been reported from previous studies (Hartshorn & Peralta 1988, Lieberman *et al*. 1996) though without sufficient data for making quantitative, spatially explicit analyses of beta-diversity. Floristic patterns quantified from the present study were from a wide distribution of plots replicated along multiple gradients to the extent feasible.

Turnover in species composition (beta-diversity) observed from ordination and correlogram plots showed strong spatial patterns that vary with both environmental and geographical distance. Our analyses identified significantly positive spatial autocorrelation for floristic composition and environmental factors up to 13 km distance. A steep decline in floristic and environmental similarity up to 4 km and significantly negative correlations after 40 km were comparable to floristic differences reported from Panamanian forest plots (Pyke *et al*. 2001, Condit *et al*. 2002). These parallels are notable considering seasonal and intermittent drought (e.g., El Niño events) occurs with greater severity across the Panama Canal Watershed in addition to complex geological substrates found in this area (Pyke *et al*. 2001). Soil textural and climate variation with elevation differences over lengthy gradients for the present study area likely explain similar floristic patterns.

Relatively moderate soil and climate differences in the present study area were significantly related to forest composition after accounting for the effects of geographical distance. Geographical distance was not a strong factor once controlling for statistically significant soil variables and elevation that is correlated with multiple environmental factors. For further discussion, we focus attention on spatial variation in forest composition and soil differences, with more general reference to significant climate and geographical variation.

Variation in soil chemical and physical properties measured from forest plots were comparable to values reported from other published studies for this region. The range of extractable cation and P concentrations was not substantially different from forest soil units analyzed at the La Selva Biological Station (Sollins *et al*. 1994). An exception was K concentrations that were low on average for our plots (0.08 cmol(+)/kg ± 0.04) compared to upland soil substrates analyzed from similar depths at La Selva (0.80 cmol(+)/kg ± 0.69) (Sollins *et al*. 1994). Grieve *et al*. (1990) found a corresponding increase in sand and organic matter with a gain in elevation and a decreasing trend for clay content from six forest sites sampled near our plots. The lack of a significant correlation between elevation differences and soil pH, P, and extractable cations in our data was also in agreement with Grieve *et al*. (1990).

From a land use perspective, the small number of plots on more nutrient rich alluvial soils reflects markedly reduced forest cover on these sites. Old-growth forest on more recently alluviated soils was rare in the study landscape having been cleared for agriculture and trees favored for lumber (e.g., *Terminalia oblonga* and *Carapa guianensis*) during colonization (Nuhn & Peréz 1967).

Factors influencing soil moisture and drainage are particularly important to forest composition in areas of high rainfall (Sollins 1998). Floristic variation for trees and palms, both together and with a separate matrix for palm species was significantly correlated with sand, clay and soil organic content. Foothills and lowland floristic groups observed along ordination axes and correlation comparisons confirm high species turnover with strong differences in soil texture also reported from Amazonian rain forest studies (ter Steege *et al*. 1993, Duivenvoorden 1995, Duque *et al*. 2002, Phillips *et al*. 2003). Lowland floristic groups on primarily clay soils showed less distinctive textural differences (Fig. 5). However, a categorical comparison between plots from the two lowland floristic groups and a distance matrix from all soil variables resulted in a significant difference ($P < 0.05$) using Multi-response Permutation Procedures (Mielke 1984, McCune & Grace 2002). Turnover in floristic composition in the lowlands also reflects a gradual transition to from areas of continuously high rainfall to seasonally lower precipitation. Locations with < 80 mm of precipitation for one month coincide with the *Q. paraensis* floristic group.

Floristic variation with respect to soil chemical properties was compared primarily for low fertility Inceptisols and Ultisols, characteristic of remaining forest. Lack of a statistically significant trend between soil chemical factors and floristic variation (*e.g.*, trees and palms combined) was not surprising under conditions of low variation in soil chemical composition. Phillips *et al.* (2003) found that large difference in soil nutrient status was significantly related to trees species composition from forest plots in south-eastern Peru. Cation concentrations across a 10,000 km^2 landscape averaged 7.9 cmol(+)/kg versus 0.65 cmol(+)/kg for Ca, Mg, and K summarized by Holocene and Pleistocene aged soils respectively (Phillips *et al.* 2003). Average cation concentrations in the present study area (1.27 cmol(+)/kg) were indicative of more highly leached Pleistocene aged soils also deficient in phosphorous(*also see* Marrs *et al.* 1988 and Grieve *et al.* 1990). In summary, canopy tree species turnover for *tierra firme* sites seems unlikely to be strongly linked to small variations in soil chemical properties - as noted from studies of upland forest in the Columbian Amazon (Duivenvoorden 1995, Duque *et al.* 2002). The likelihood of a link is stronger when gradients are longer and encompass extreme values, as reported from Phillips *et al.* (2003) and Duque *et al.* (2002).

Mid- to upper-canopy palms, on the other hand, showed a significant relationship with soil cations Mg and Ca and pH and total acidity. Our data suggest that soil physical properties and chemical composition of specific cations are important to palm distributions. These results are in agreement with Clark *et al.* (1995) who found that palm species (*e.g.*, *E. precatoria*, *I. deltoidea* and *S. exorrhiza*) were spatially structured according to meso-scale differences in soil types with varying chemical and textural composition. Poulsen *et al.* (2006) also found Mg and Ca concentrations were significantly correlated with palm distributions for a 1-ha plot studied in Amazonian Ecuador. Significant correlations for sand, clay and elevation and a lack of significance for K, P, pH and slope from Poulsen *et al.* (2006) corresponded surprisingly well with our results considering the wide difference in scales. Ruokolianen & Vormisto (2000) reported more generalized palm distribution patterns at the landscape-scale for three of the four palm species (*W. regia* excluded) on Amazonian plots and comparisons with summed cation concentrations (i.e., Ca, Mg, K and Na).

However, species presence-absence data were used and no comparisons were made with soil textural conditions. From our study area, *S. exorrhiza* and *W. regia* abundance decline substantially on increasingly sandy-loam soils above 300 m elevation while *I. deltiodea* and *E. precatoria* remain consistently abundant to 900 m.

After accounting for geographical distance in statistical analysis, complex physiographic conditions and changes in soil substrates across Caribbean lowland and foothills environments were significantly correlated with forest beta-diversity. Conversely, geographical distance was a less important to species distributions once accounting for significant soil and elevation variables for this landscape. Pyke *et al*. (2001) also concluded that dispersal limitation is likely secondary to environmental drivers at the landscape-scale. In contrast, recent analyses for Panamanian plots by Chust *et al*. (2006) showed stronger support for a dispersal hypothesis from correlation comparisons and model fitting. An explanation for differing conclusions is that geographical distance is perhaps a better predictor of floristic patterns without measurements of underlying soil gradients, also acknowledged by Chust *et al*. (2006). From these comparisons, we find greater support for a niche-assembly hypothesis as the principal driver of forest beta-diversity in this landscape. These observations can aid integrated modeling of forest compositions with the caveat that differences between life-forms observed (*e.g.*, canopy trees versus palms) respond differently to the physical environment. Quantitative comparisons between soil and rain forest composition in neighboring Nicaragua or from Costa Rica's Osa Peninsula where similar tree and palm species coexist would provide further insight into ecological factors driving beta-diversity.

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Tables

TABLE 1. Summarized soil chemical and physical properties from 0.25-ha old growth forest plots (n = 127) in northeastern Costa Rica.

	Mean	**Range**	**SD**
Ca (cmol(+)/kg)	0.73	0.06-11.02	1.78
K (cmol(+)/kg)	0.08	0.02-0.28	0.04
Mg (cmol(+)/kg)	0.46	0.82-5.59	0.95
Sum of Ca, K, Mg	1.27	0.19 - 15.2	2.72
P (mg/kg)	2.70	0.47-15.1	1.92
Total acidity (cmol(+)/kg)	2.88	0.10-7.26	1.23
pH	4.57	3.83-6.40	0.38
Organic matter – OM (%)	8	1.70-23.9	4.15
Sand (%)	37	8-81	21.29
Silt (%)	17	7-42	5.56
Clay (%)	46	4-78	20.64

TABLE 2. A correlation matrix and Pearson coefficients from Modified t-tests comparing soil and terrain variables from plots. Significant correlations ($P < 0.05$) in black were computed using reduced degrees of freedom (effective sample size) corrected for spatial autocorrelation (Dutilleul *et al.* 1993).

	Acidity	Ca	K	Mg	P	Sand	Silt	Clay	OM	Slope	Elev
pH	**-0.53**	**0.81**	**0.44**	**0.82**	**0.22**	-0.02	**0.61**	-0.14	-0.20	0.07	0.05
Acidity		-0.29	-0.16	**-0.27**	0.01	**-0.41**	-0.08	**0.45**	**-0.28**	-0.14	**-0.45**
Ca			**0.68**	**0.95**	**0.44**	-0.14	**0.63**	-0.03	-0.26	0.07	-0.11
K				**0.60**	**0.40**	**0.24**	**0.41**	**-0.36**	0.20	0.15	0.23
Mg					**0.53**	-0.18	**0.71**	-0.01	-0.27	0.00	-0.15
P						-0.11	**0.26**	0.04	0.01	-0.18	-0.20
Sand							**-0.25**	**-0.97**	**0.80**	0.33	**0.87**
Silt								-0.02	**-0.31**	0.07	-0.12
Clay									**-0.74**	-0.36	**-0.87**
OM										0.18	**0.78**
Slope											0.33

TABLE 3. Summarized climate and terrain attributes associated with forest plots from digital grids.

	Mean	**Range**	**SD**
Elevation (m)	267	41-1222	264
Slope (%)	9	0-53	9
Mean monthly temperature (°C)	25	20-26	1.1
Temperature seasonality (SD * 100)	663	515-762	54
Min. monthly temperature (°C)	20	15-21	1.2
Annual precipitation (mm)	3976	2853-4530	313
Rainfall seasonality (CV)	32	27-59	6
Min. monthly precipitation (mm)	144	51-187	34

TABLE 4. Mantel correlations tests comparing environmental and floristic variability. Simple (^{a}Mantel *r*) and Partial Mantel tests (^{b}Mantel *r*) accounting for geographic distances are shown in parallel. Comparisons between floristic composition and log geographical distance is shown controlling for environmental factors in parentheses. Significance levels were determined from 999 matrix randomizations (***P < 0.001, **P < 0.01, *P < 0.05).

	Trees and palms		Palms	
	^{a}Mantel *r*	^{b}Mantel *r*	^{a}Mantel *r*	^{b}Mantel *r*
Ca	0.05		0.20**	0.19**
K	0.02		0.07	
Mg	0.04		0.19**	0.18**
P	0.05		0.07	
Total acidity	0.06		0.20**	0.19**
pH	0.03		0.17**	0.16**
Organic matter	0.34***	0.31***	0.22***	0.20***
Sand	0.41***	0.35***	0.34***	0.28***
Silt	0.09		0.13*	0.13*
Clay	0.54***	0.50***	0.35***	0.31***
Elevation	0.54***	0.51***	0.29***	0.20***
Slope	0.14*	0.14*	0.10	
Mean monthly temperature	0.48***	0.46***	0.32***	0.28***
Temperature seasonality	0.37***	0.36***	0.25***	0.23***
Min. monthly temperature	0.49***	0.47***	0.34***	0.31***
Annual precipitation	0.29***	0.26***	0.28***	0.23***
Precipitation seasonality	0.29***	0.26***	0.11**	-0.02
Min. monthly precipitation	0.19***	0.10*	0.10*	-0.02
Geo dist	0.28***			0.24***
Geo dist (Elev)	0.16***		(Elev)	0.10***
Geo dist (Elev + clay)	-0.03		(Elev + clay)	0.10*
Geo dist (Elev + sand)	-0.02		(Elev + Mg)	0.05

Figures

FIGURE 1. Map of forest plots located between the Caribbean lowlands and foothills of the Central Volcanic Range of northeastern Costa Rica. From left to right and top to bottom figures are; forest and non-forested areas (white) that are mainly pasture and croplands, DEM elevations, mean annual temperature (T), temperature seasonality (described in text), total annual precipitation (P), and minimum monthly precipitation. The Central Volcanic Range spans the lower left corner of figures.

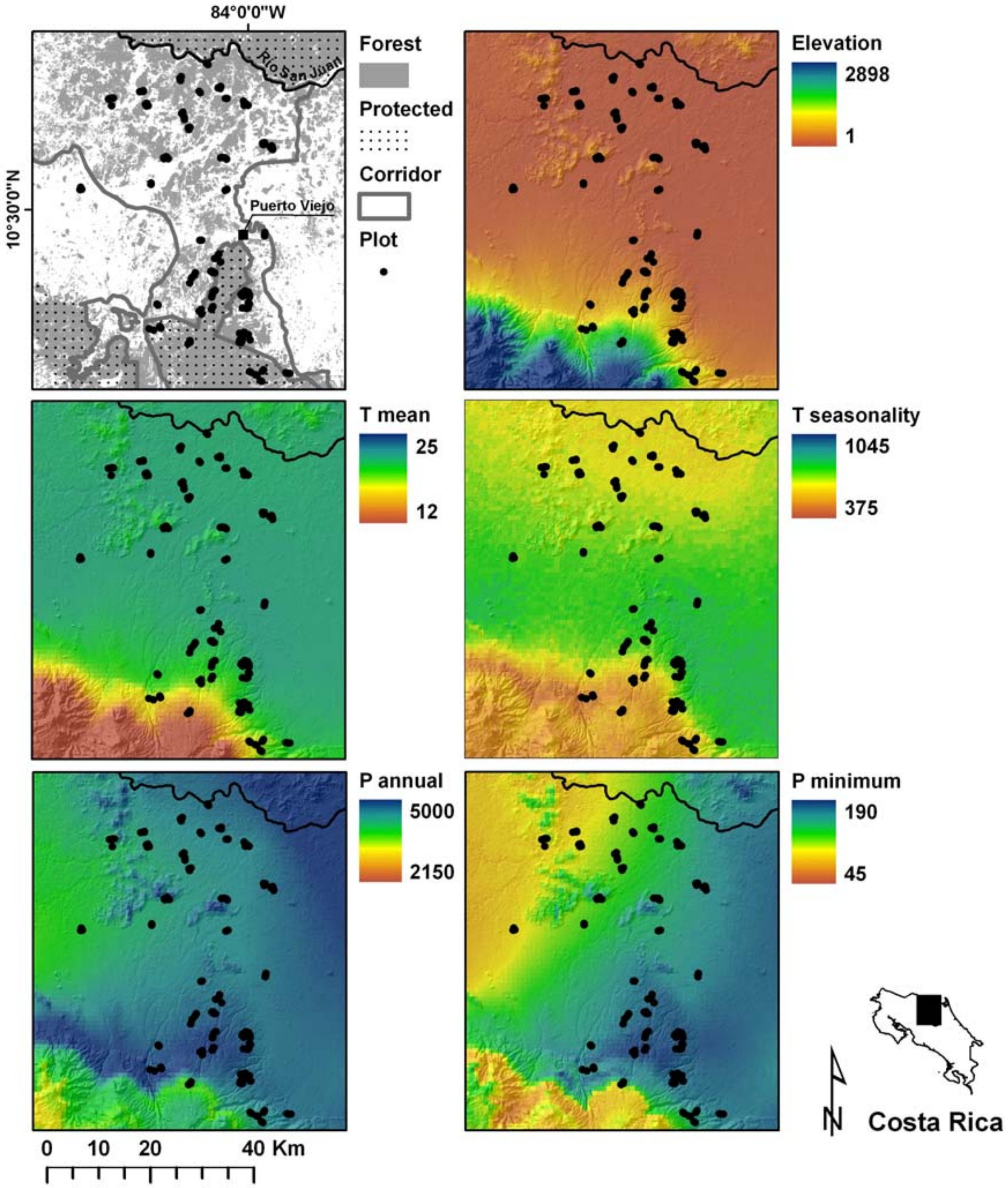


FIGURE 2. NMS ordinations of plot data overlaid with floristic groups from cluster analysis termed foothills forest (Δ), and *Pentaclethra macroloba* (○) and *Qualea paraensis* (■) forest in the lowlands. Plot distributions along ordination axes are generally determined by *Tapirira guianensis* (Pearson *r* = - 0.40, axis 1), *Q. paraensis*, *Euterpe precatoria*, *Socratea exorrhriza, Welfia regia* (Pearson *r* > -0.50, axis 2), *P. macroloba* (Pearson *r* = -0.85, axis 3) and *Vochysia allenii* (Pearson *r* = 0.51, axis 3).

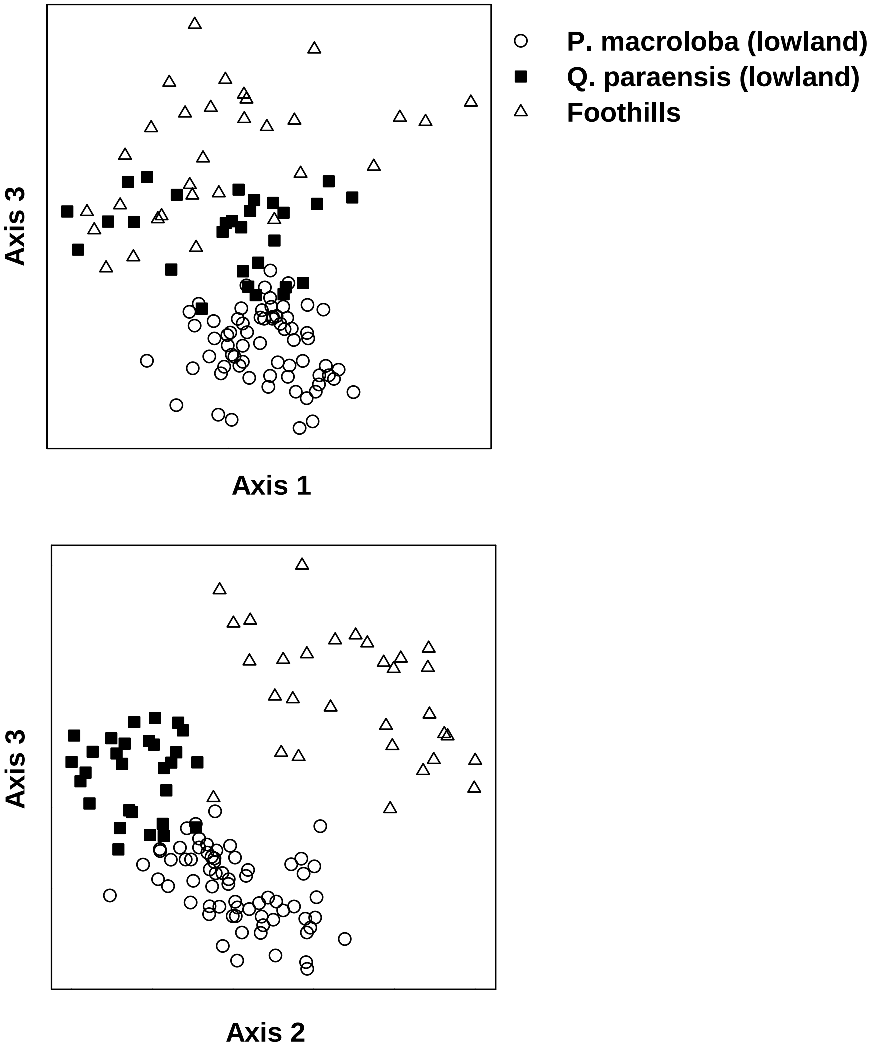


Figure 3. Dominance-diversity curves of the logarithm of total and ranked species abundances. Curves indicate a high density of a few dominant species for *P. macroloba* forest (Black) relative to other floristic groups. Lower densities of dominant species are shown for mixed floristic compositions in *Q. paraensis* (Dark grey) and foothills (Light grey) forest. Twice the amount of area sampled for *P. macroloba* forest helps explain a greater number of species shown for this group (x-axis).

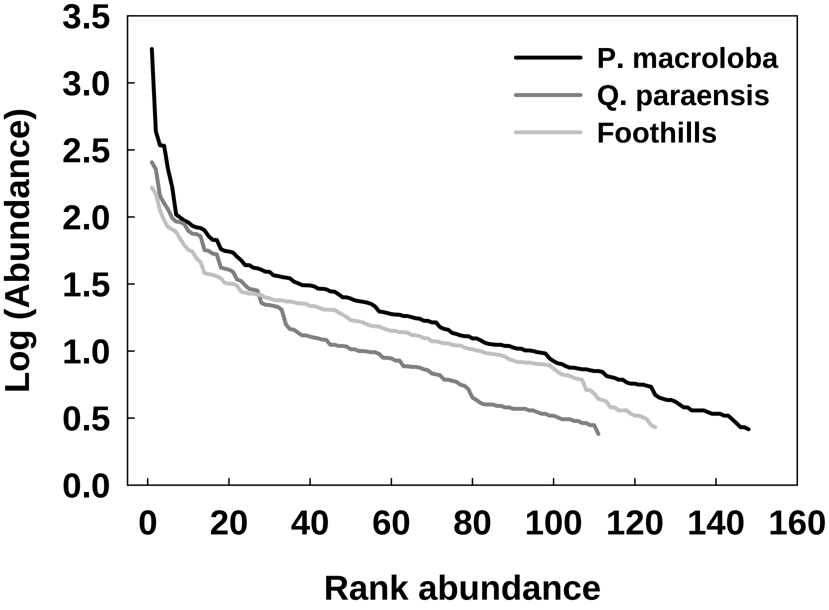


FIGURE 4. Spatial autocorrelation coefficients of forest plot pairs and 22 geographic distance classes at 3 km increments after the first 2 classes. The x-axis shows the minimum geographic distance for each class. Parallel Mantel comparisons are with distance matrices from, a) floristic composition (■), and elevation, temperature seasonality and minimum monthly precipitation combined (○), and b) floristic composition (■) and clay and sand combined (Δ). Symbols above (+) and below (-) the dotted lines are significant correlations ($P < 0.05$).

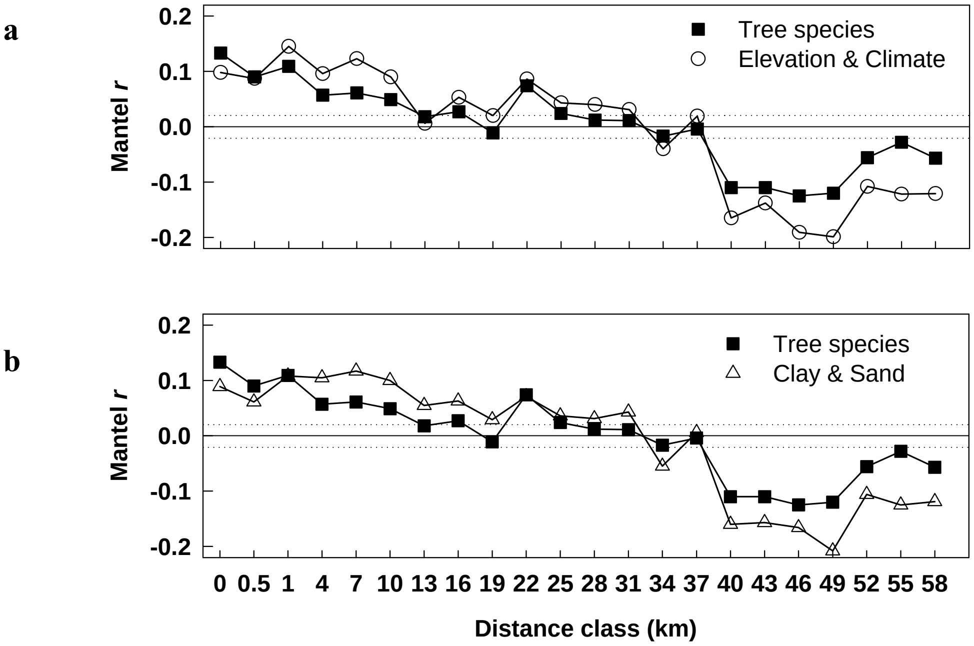
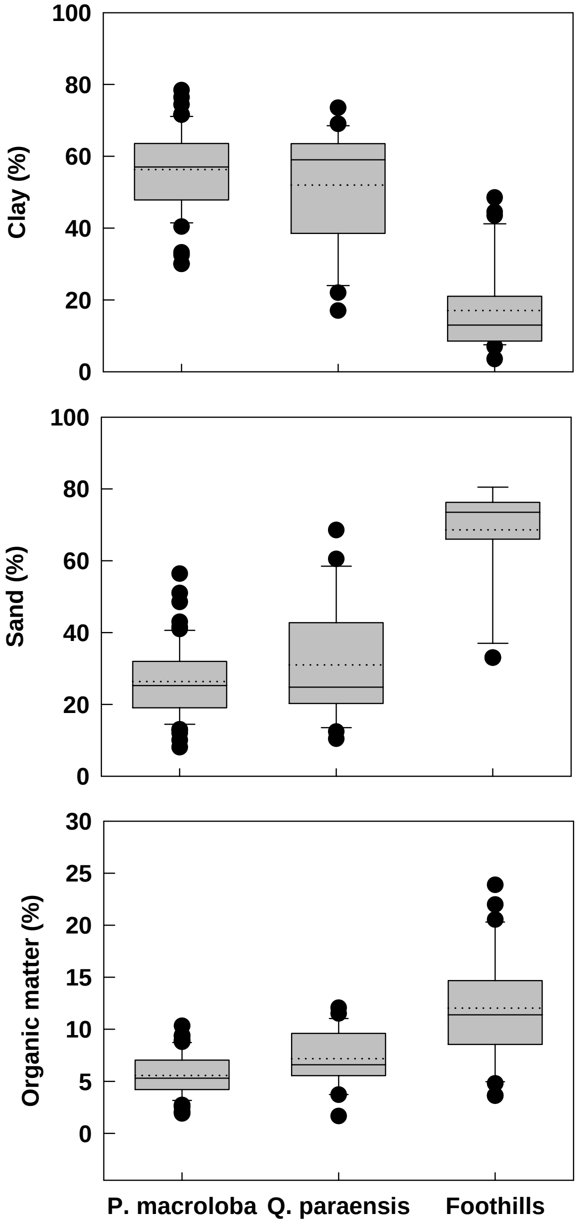


FIGURE 5. Box plots of significant soil physical properties of percent sand, clay and organic matter on plots from each floristic group. Boxes are to the 75th percentile and error bars mark the 90th percentile range. Group means and medians inside boxes are shown with a dotted and solid line respectively. Outlying points are in back.



Chapter 3

Integrating Landsat TM and SRTM-DEM derived variables with decision trees for habitat classification and monitoring in complex neotropical environments

Abstract

Reducing the loss of habitats important to biodiversity by the year 2010 is a principal objective of the 1992 Convention on Biological Diversity (CBD). Remote sensing techniques are a primary tool for monitoring the status of tropical forests with potential to make a vital contribution towards meeting CBD and other environmental objectives. Detailed landcover data are lacking for most wet tropical environments that present special challenges for data collection. For this study, we compare the accuracy of several decision tree (DT) classifiers to map 32 landcover types of varying ecological and economic importance over an 8,000 km^2 study area, including a conservation corridor, in northern Costa Rica. We assessed two computationally fast multivariate DTs, *QUEST* and *CRUISE*, with unbiased classification rules and linear discriminant node models for integrated vegetation mapping and monitoring. Ten floristic alliances were derived from a cluster analysis of data from 144 georeferenced forest plots and IUCN wetland categories. Structurally-defined forest types included riparian forests, tree plantations and regrowth areas, in addition to agricultural land use categories. A set of 35 variables hypothesized to be related to vegetation composition were assessed from SRTM-DEM derived terrain variables, WorldClim bioclimatic surfaces, and Landsat TM images from 1986 and 2001. Predictor variables related to floristic alliances and important to classification accuracy were selected using statistical methods with *"Random Forest"* classification trees.

Of the techniques examined, the *QUEST* classifier was the most efficient and accurate method to integrate Landsat TM bands with other geospatial data. A resulting set of 12 spectral and spatial predictor variables produced overall cross-validation accuracies of 93%±7% and 83%±15% from *QUEST* and *CRUISE*, respectively. Error matrices were summarized from a subset of 4 image tiles used to improve computing speeds. Comparisons using a random selection of training and test set pixels for the entire landscape yielded lower test set accuracies for *QUEST* (85%) and *CRUISE* (77%) demonstrating a positive affect of image subsets on accuracy. A comparison between 1986 and 2001 image dates revealed specific habitats vulnerable to agricultural conversion, in addition to locations with increased land use intensities and urbanization. Decision tree classifiers capable of combining globally available data resources with locally-generated field data are accurate and highly adaptable for monitoring vegetation alliances and forest structural types important to biodiversity and other ecosystem services in this complex wet tropical environment.

Keywords: Decision trees, Biodiversity, Costa Rica, Landcover change, SRTM-DEM, Landsat TM

1. Introduction

Validated methods to discriminate diverse tropical vegetation types with remotely sensed data have become progressively more important following the 1992 International Convention for Biological Diversity (CBD) (UNEP, 1992; Nagendra & Gadgil, 1999). Reducing rates of native habitat loss prior to the year 2010 is a principal objective established by the CBD. The 1992 United Nations Framework Convention on Climate Change targets aforestation and reforestation areas as carbon sinks that can also restore a level of forest connectivity and habitat within highly fragmented landscapes (Lamb et al., 2005). Secondary forest and replanted stands play an increasingly important role to meet the demand for wood fiber, carbon sequestration services and can provide habitat for biodiversity (Castro et al., 2003). National conservation strategies towards these ends are linked to environmental services such as watershed protection, climate stabilization and other forest resources important to humans (Millennium Ecosystem Assessment, 2005). Multitemporal information regarding the extent of habitat types, regeneration areas and landcover dynamics for tropical regions is needed to achieve diverse conservation goals.

Creating suitable landcover information for natural resource planning and prioritizing conservation activities will require methods to integrate data from a variety of Earth observation systems (Kerr & Ostrovsky, 2003). Acceptable approaches must ultimately be ecologically valid and operationally feasible (Defries & Townsend, 1999; Brown de Colstoun et al., 2003). With this study, we examine the potential for discriminating tropical rain forest and other landcover types with decision tree (DT) classifiers adapted to heterogeneous landscape conditions in Central America. Accelerated deforestation since the 1950s has left scattered habitat remnants and regrowth areas amid agricultural production lands over much of Central and South America (Houghton, 1994; Defries et al., 2005; Mayaux et al., 2005).

Highly mixed forest and landcover conditions add complexity to these landscapes which are important to the ecological function of remnant and regenerating habitats (Laurance & Bierregard, 1997; Holl & Kappelle, 1999; Ricketts, 2001).

Differentiating floristic categories based on dominant or characteristic species, in addition to landcover related to disturbances and agricultural development in a priority conservation area is a primary objective for this study. Spectral features from Landsat Thematic Mapper (TM) and Enhanced Thematic Mapper (ETM+) images have been shown capable to discriminate some rain forest types and secondary forest successional stages (Foody & Hill, 1996; Lobo & Gullison, 1998; Nagendra & Gadgil, 1999; Pedroni, 2003; Lu et al., 2003). However, vegetation classification can be limited by traditional satellite image based approaches when ecologically important differences in forest structure and composition are spectrally similar (Sader et al., 1989; Lu et al., 2003; Helmer et al., 2002; Castro et al., 2003). Integrating biophysical factors related to natural vegetation patterns and human land use with satellite data can potentially improve class separability (Ferrier et al., 2002; Pedroni, 2003).

Non-parametric DTs have been shown to be more capable than other methods for integrating data to solve complex ecological classification problems (De'ath & Fabricius, 2000; Franklin, 2003), but are relatively unexplored for mapping highly varied tropical landscapes (*but see*, Muchoney et al., 2000). Decision tree classifiers resemble a dichotomous key constructed for a known set of samples (i.e., training data) and attributes (i.e., predictor variables) used to characterize each sample. The process follows that class training samples are recursively split at a series of nodes in a tree based on a selected attribute and threshold value for splitting classes into increasingly homogeneous sub-groups (Breiman et al., 1984). Trees are grown until class samples reach a terminal node defined by the training sample label. Classification rules developed from training data are then applied to determine class membership for many unseen cases using characteristic spectral features, as is practiced with remote sensing applications (Friedl & Brodley, 1997).

Advantages of DTs are their versatility to integrate numerical and categorical variables into vegetation classifications free of distributional assumptions (Brieman et al., 1984; Guisan & Zimmerman, 2000). In many cases, parametric statistical models are not suitable for data integration because of non-linear relationships and correlation among variables (Friedl & Brodley, 1997; Franklin, 2003). Decision tree outputs can be interpreted and are instructive for identifying important variables related to vegetation structure and composition (Urban et al., 2002; Joy et al., 2003; Gislason et al., 2006). Graphical or numerical outputs can elucidate complex conditional relationships between variables and individual categories that are infeasible with traditional parametric approaches (Urban, 2002). DTs may also reduce the training time required by other machine learning techniques, such as artificial neural networks and support vector machines, while attaining similar accuracies (Pal & Mather, 2003; Pal, 2005).

Limitations to DT classifiers include the instability of trees to outliers or small changes in the training data (Miller & Franklin, 2002), in addition to requiring a large number of training samples for tree construction (Joy et al., 2003). Pal and Mather (2003) note that DTs may not exceed accuracies over maximum likelihood or neural network classifiers using high-dimensional data for landcover classification (e.g., hyperspectral imagery), but show improved results with ETM+ imagery and fewer spectral bands.

Despite their potential drawbacks, DT classifiers have shown improved accuracies over other techniques for mapping national and global-scale landcover with the advanced very high resolution radiometer (AVHRR) and moderate resolution imaging spectroradiometer (MODIS) (Friedl & Brodly, 1997; Defries et al., 1998; Muchoney et al., 2000; Hansen et al., 2000; Friedl et al., 2002). Brown de Colstoun et al. (2003) and Joy et al. (2003) obtain favorable accuracy at local and landscape scales for classifying mixed broadleaf and coniferous forest types using Landsat ETM+ data. Joy et al. (2003) demonstrate that integrating elevation, slope and aspect variables derived from a digital elevation model (DEM) improve accuracy for classifying coniferous forest composition categories.

An increased availability of multispectral and geographic information of known quality improves the potential for integrating data to map and monitor floristically defined forest categories (Gislason et al., 2006). Landsat TM’s >20 year image archive is a primary source of repeated Earth observations at a ~30m pixel resolution, particularly important for obtaining relatively cloud free images in wet tropical areas. The recent availability of digital elevation data at a 3-arc second spatial resolution from the Space Shuttle Radar and Topography Mission (SRTM) dramatically improves data resources for all tropical regions

(Hofton et al., 2006). A DEM is often a primary data source for deriving terrain variables related to vegetation composition (Franklin, 1995; Miller & Franklin, 2002). The WorldClim data set, used for this study, combines SRTM-DEM elevations with global meteorological records to improve monthly temperature and precipitation surfaces at a ~1 km grid cell size (Hijmans et al., 2005). These data resources represent improved low-cost information for repeated applications to map and monitor tropical habitats important to biodiversity and other conservation objectives.

An added consideration, important to this study, is that classical "niche theory" and gradient analysis is central to DT applications for predictive vegetation modeling and pattern recognition (Franklin, 1995). Niche theory posits that ecological communities and their component vegetation are structured along environmental gradients that are important to making predictions beyond sampled locations (Whittaker, 1967; Miller & Franklin, 2002). Predictive approaches to vegetation modeling (e.g., DT classifiers) rely on the interdependence between plant species distributions and environmental differences (Franklin, 1995). Therefore, similar vegetation compositions are expected to occur on sites with comparable climate, soil factors, and other terrain conditions (Tuomisto et al., 2003a). In contrast, biogeographical factors, random events or disturbances and dispersal limitations can significantly influence tropical tree species composition (Condit, 1996). In the event that disturbances, common to neotropical rain forest (Hartshorn, 1980; Hubbell et al., 1999), and seed dispersal are highly random occurrences, tree species similarity is expected to decline logarithmically with increased geographic distance among sites (Hubbell, 2001; Condit et al., 2002). Consequently, geographic distance among vegetation samples has been used to substitute for potentially unmeasured variables to predict species distributions in temperate and topical regions (Franklin, 1998; Chust et al., 2006).

With this study, we consider a framework to combine multitemporal satellite and geographic information with ground vegetation data for enhanced landcover mapping and monitoring. Our first objective is to determine which spectral and spatial variables contribute the most to classification accuracy for mapping priority floristic alliance categories. Alliance is defined here as floristic categories based on existing vegetation of similar physiognomy, characterized by dominant tree species or other diagnostic vegetation (Jennings et al., 2004). The *Random Forest* decision tree method (Breiman, 2001), discussed below, is used to define predictor variables in a heuristic manner leading to accurate classifications with DTs. A second objective is to compare two robust and computationally efficient multivariate DT classifiers via cross-validation accuracy using sub-set of predictors. Our ultimate goal is to select a suitable approach for detailed monitoring of landcover trends in priority conservation areas. Landcover data generated with DT classifiers from paired 1986 and 2001 Landsat TM images were used to quantify changes important to the CBD and other objectives to maintain regional floristic diversity.

2. DT classifiers

Recent innovations in DTs have introduced unbiased variable selection, multi-way splitting rules and multiple-classifier techniques which are shown to be accurate with a variety of datasets (Loh & Shih, 1997; Kim & Loh, 2001; Ham et al., 2005; Gislason et al., 2006). We compare the accuracy of two differing multivariate DT approaches with flexible features for data integration which are expected to produce accurate classifications for complex landcover conditions. The *Quick Unbiased Efficient Statistical Tree* (*QUEST*) by Loh and Shih (1997) and the *Classification Rule with Unbiased Interaction Selection and Estimation* (*CRUISE*) by Kim and Loh (2001) were selected as computationally fast and unbiased multivariate techniques with accuracies comparable to other conventional DT methods (Lim et al., 2000; Kim & Loh, 2001; Pal & Mather, 2003).

Friedl and Brodley (1997) suggest that multivariate DTs may enhance vegetation classifications by using a separating hyperplane to form decision boundaries among categories and linear discriminant model fitting. Conventional DTs, similar to *Classification and Regression Trees* (*CART*) (Breiman et al., 1984), frequently use exhaustive search routines where each response category and set of variables is evaluated to select those leading to increased class homogeneity. Biased procedures may use predictors that fit the data to a model well, but are poorly suited to classifying many new samples (Loh & Shih, 1997). Further, an exhaustive variable and split selection approach is computationally demanding (Lim et al., 2000) and a limitation for remote sensing applications where many categories and predictors are present.

QUEST performs successive binary splits (“1D”) at each node that resemble *CART* trees (Breiman et al., 1984), but instead use ANOVA *F*-tests for numerical variable selection and a linear discriminant analysis (LDA) for split-point selection from training samples.

Variables with the largest *F*-statistic are selected and an LDA for ordered variables is used to find the split-point value *c* that follows $\sum_{k=1}^{K} \boldsymbol{a}_k \boldsymbol{x}_k \leq c$, where $\boldsymbol{x}_k$ is a vector of attributes for *K* selected features. LDA yields vector $\boldsymbol{a}$ from the linear discriminant function to determine *c* (Loh & Shih, 1997). *QUEST* can also be run with exhaustive variable search or splitting routines for constructing *CART*-like models (Loh & Shih, 1997). *CRUISE*, on the other hand, is capable of a bivariate node splitting method ("2D") and applies a Box-Cox transformation before performing a LDA to select the best pair of splitting variables (Kim & Loh, 2001). *QUEST* may therefore produce errors for discriminating class samples that show non-uniform distributional patterns that are normalized by the *CRUISE* procedure (Kim & Loh, 2001). Each of these methods has been shown to produce compact and accurate trees for a variety of datasets (Lim et al., 2000).

Important variables leading to accurate classification for vegetation alliance and other categories were desired for comparison of *QUEST* and *CRUISE*. *Random Forest* (Breiman, 2001) classification trees provide a powerful set of analytical procedures useful for detecting important multispectral features and geographical information for integrative landcover classification (Gislason et al., 2006). We use the *Random Forest* package within the R (v. 2.3.1) statistical software (R Development Core Team, 2006) for classification model runs with forest plots labeled as alliance categories from prior hierarchical cluster analysis (Sesnie et al. in review). The *Random Forest* procedure computes importance metrics that assess each variable's contribution to decreasing classification errors. *Random forest* DTs are similar to *CART* models (Breiman et al., 1984), but are considered unbiased classifiers that produce multiple trees by drawing a random bootstrap training sample with replacement from approximately one-third of the data (Breiman, 2001). Trees are independently constructed with each bootstrap training sample and are then aggregated by taking a "majority vote" for class prediction, a process known as "bagging" (Breiman, 1996). A set of classification trees is defined as $\{h(x,\Theta_k), k = 1,...,\}$, where the $\{\Theta_k\}$ are independent identically distributed random vectors and each tree yields a single unit vote for the most popular response category at input vector x (Breiman, 2001). For error estimation, samples left "out of bag" (OOB) during training are run down an individual tree generating an error value for all categories at each iteration. Prediction errors are aggregated from the number of trees requested to generate an overall OOB error estimate.

A feature important to this study is that each predictor variable is randomly chosen, usually 2 or 3 at each node selecting the one leading to the best split (Breiman, 2001). Variables can be individually permuted for a tree while leaving others unchanged to provide a measure of a predictor's contribution to accuracy. Prediction error generated for data out of bag with the variable removed provides a measure of its importance. We use importance metrics to select a subset of predictors from a large set of potential variables related to floristic alliances.

3. Study landscape

We confine our analysis to an 8,000 km^2 landscape including the 2,425 km^2 San Juan – La Selva (SJ-LS) Biological Corridor between protected areas in northern Costa Rica and Nicaragua (Figure 1). The corridor initiative seeks to retain private forests as linkages between protected areas in addition to vegetation types representative of the region's floristic diversity (Chassot & Monge, 2002). Land use histories outside protected areas in this region are characterized by a rapid colonization period with high forest conversion to cattle pastures up to the 1980s, followed by a post-settlement period of intensified agricultural use (Butterfield, 1994). Remnant forest and swamplands consist of small fragments of a few hectares in size to large contiguous forest patches >1,000 ha along the boarder with Nicaragua. Natural forests are interspersed with pasture systems, perennial and seasonal crops, tree plantations and small patches of secondary forest re-growth in addition to riparian forest remnants (i.e., narrow forest corridors, often disturbed forest edge environments, retained along rivers and streams) (Read et al., 2001). The study area is one of three large concentrations of privately owned native forest in Costa Rica and has been the focus of national reforestation and management programs since the mid-1980s (Watson et al., 1998). Costa Rican territory represents 80% of the analysis area and the remaining 20% is part of Nicaragua's Indio Maíze Biological Reserve (Figure 1).

The biophysical environment and vegetation are strongly influenced by elevation which ranges from sea level to >3000m over the landscape (Lieberman et al., 1985; Lieberman et al., 1996). The lowlands are a mixture of steep hilly terrain, alluvial terraces, and flat swamplands interrupted by hills reaching 400m elevation. Monthly temperature averages near 24°C in the lowlands, but temperatures decrease to as low as 10°C at the highest elevations in the Central Mountains (Lieberman et al., 1996). Annual precipitation ranges from 4,000mm in the central portion of the study area (Hartshorn & Peralta, 1988; Grieve et al., 1990) to <2,500mm in the western lowlands according to precipitation data by Hijmans et al. (2005). Much of the eastern lowlands and the foothills have consistently high rainfall throughout the year. Seasonally lower precipitation occurs in the western lowlands and southwestern slope of the Central Mountains, with average monthly rainfall ≤100mm for 1 to 3 months.

4. Floristic alliances & landcover

With this study, we consider the use of floristic alliances to characterize forest observed from plot data and wetland types. Floristically defined categories are not widely applied for mapping forests in Costa Rica given its species-rich vegetation and complex terrain (Hammel et al., 2004). More often, Holdridge Life Zones (Holdridge, 1967) are employed relating region scale vegetation to average annual climatic conditions, though the system does not include seasonal or topographic factors considered important to floristic patterns (Blasco et al., 2000; Hammel et al., 2004). A more thorough review of vegetation classification systems that have been applied in Costa Rica is provided in Kappelle et al. (2003). Alliance-type classifications have had some historical use in Costa Rica. Mapped vegetation associations for the Atlantic lowlands by Nuhn and Pérez (1967) provide detailed forest and wetland types c. 1960 using dominant trees or other vegetation at a 1:60,000 map scale. Associations (term used by the authors) were mapped from field plots, aerial photo interpretation and information from individuals familiar with remote vegetation. A comparison of historical maps and recent satellite images reveals that once extensive alluvial flood plains forests, dominated by *Terminalia oblonga,* have been nearly eliminated from the lowlands as well as other forest areas (personal observation). Present strategies to map and monitor Central American vegetation are insensitive to floristic community changes at scales below the regional level (*But see* Chust et al., 2006).

To make DT classification comparisons, we defined a total of 32 landcover categories from three general groups that were identified from previous studies (Sandner & Nuhn, 1966; Nuhn & Pérez, 1967; Holdridge, 1967; Pedroni, 2003; Sesnie et al., in review) (Table 1). The first group contains seven floristic alliance categories that were derived by Sesnie et al.

(in review) from multivariate cluster analysis of 144 forest plots and canopy tree species data located across the study landscape (Figure 1). Three IUCN wetland categories were used consisting of extensive palm swamps, forested swamps and herbaceous swamps that also included other non-forested floodplain vegetation. Wetland categories were consistent with areas mapped on Costa Rica's 1:50,000 topographic sheets and categories by Nuhn and Pérez (1967). Table 1 provides a list of species indicative for each floristic alliance. For elevations >1400 m, where field data are lacking, generalized Holdridge Life Zones were used to characterize old-growth forest conditions. A second group of forest structural types were: 1) *charral* (native regrowth dominated by shrubs and herbaceous vegetation), 2) secondary forest (primarily tree dominated forest regrowth on abandoned pastures), 3) reforested areas (tree plantations) and 4) riparian forests (linear forest remnants located along waterways). The third group included common agricultural land use types, urbanized centers, water, rock and exposed soil associated with horticulture crops (Table 1).

5. Materials and methods

5.1 Vegetation and training data

Forest alliance categories were defined from a total of 144, 0.25-ha and 1.0-ha plots (seven account for previously measured 1-ha plots) that were established between 2003 and 2004 along elevation and precipitation gradients across the study area. Trees ≥30 cm dbh (1.37m above base) and arborescent palms and ferns ≥10 cm dbh were measured to include species likely to reach the mid- to upper-canopy strata (Lieberman & Lieberman, 1994). Plots were located at a minimum distance of 150m from forest edges and at least 300m from each other on upland sites (i.e., non-swampy areas) in dispersed old-growth forest fragments across the study landscape (Figure 1). Therefore, inter-plot distances vary between from 300m and ~100km. Many forest areas sampled had some selective logging although highly disturbed areas were avoided. Tree species encountered on more than one forest plot, 203 species in total, were used to derive forest alliance categories in Sesnie et al. (in review). Dominant or diagnostic species for each category are indicated in Table 1.

For *QUEST* and *CRUISE* DT model runs, supervised classification procedures were used by selecting a set of training pixels representing each landcover type from TM images and grids (i.e., predictors). Training sites were obtained from the following sources; 1) ~1000 field locations for forest and landcover types (Table 1) referenced with a Trimble

GeoXT global positioning system (GPS) collected across the study area during 2003-2004 (includes forest measurement plots mentioned above), 2) high spatial resolution aerial photographs from years 1986/7, 1992, 2003, and a Quickbird image from 2004, and 3) 82 additional georeferenced forest inventory locations with tree species data representing mainly lowland alliance categories. Training sites for old-growth forest at higher elevations than our plot samples are labeled as life zone categories from a digital map. Locations referenced in the field with a GPS were cross-referenced with aerial photos or a Quickbird image. The number of training pixels in each class is dependent on our ability to locate sites corresponding to image dates (Table 1).

5.2 Spectral & spatial variables

Variables were acquired or derived from February 1986 and January 2001 Landsat TM images (WRS-2 path 15, row 53), SRTM-DEM elevations, and 19 WorldClim bioclimatic surfaces (Table 2). For simplicity, we refer to Landsat TM bands as spectral variables and all others as spatial variables. SRTM elevation data (level-1 corrected, 3-arc second) was acquired from the United States Geological Survey. A small number of information voids were filled with digital elevation data derived from Costa Rica's 1:50,000 contour maps by Pedroni (2003). Each data source was resampled to a 28.5 x 28.5m grid cell size using a nearest-neighbor method to match Landsat TM pixel sizes. Other conditions such as soil characteristics and superficial geology are likely to be important, but presently exist at map scales not suitable for data integration.

Landsat TM images from 1986 and 2001 (for multitemporal landcover comparisons) were systematically processed to provide geometric and radiometric corrections prior to analyses. Images were first co-registered to a 1996 TM image that was referenced to positions on the ground by Pedroni (2003) using nearest neighbor resampling and a second-order polynomial with <3m RMSE. Positional accuracy between image dates was estimated at <15m displacement comparing locations on images to georeferenced roads and intersections recorded with the Trimble GeoXT GPS throughout the study area. The thermal infrared band 6, with lower spatial resolution (120m pixels), was removed and bands 1 to 5 and 7 were converted to top of atmosphere reflectance using calibration coefficients from Chander & Markham (2003). In the absence of atmospheric data, a dark object subtraction method was used to make radiometric corrections for each image, selecting pixels from deep water bodies to reduce effects from atmospheric scattering (Teillet & Fedosejeves, 1995). Image noise in the visual spectral bands was removed using a Minimum Noise Fraction (MNF) forward and inverse rotation (Green et al., 1988). An MNF forward rotation consists of a two cascaded principal components analysis (PCA) to segregate noise dominated signals from relatively noise-free data (Green et al., 1988). Non-correlated PCA bands with no visual noise present were used for an inverse rotation, transforming coherent data back to noise-free spectral bands. Noise corrected bands (TM 1 - 3) were combined with others that had no noise present for analyses.

Additional image enhancements were aimed at improving spectral sensitivity to forest structural and other landcover categories. The Normalized Difference Vegetation Index (NDVI) index was derived from red and near-infrared (NIR) TM bands (*NIR-Red/NIR+Red*) and added to spectral bands for analysis. NDVI is, to an extent, sensitive changes in plant biomass, vigor, and leaf-area (Jensen, 2000) that varies for forest structural and crop types in the study area (Pedroni, 2003). NDVI has been shown to yield lower values for young secondary regrowth and some even-age forest structural types (e.g., tree plantations) in comparison with advanced forest developmental stages (Sader et al., 1989; Steininger, 1996). A mean textural occurrence filter with a 3 x 3 pixel window was also applied to all spectral bands to reduce high frequency noise and within-class variance for each landcover category. A mean textural filter adjusts the center pixel of a moving window to the weighted mean of eight surrounding pixels, a process that has shown to improve spectral separation between tropical forest categories (Hill & Foody, 1994; Salovaara et al., 2005).

Elevation data from the SRTM-DEM and topographic features associated with soil drainage and moisture, and solar radiation were assumed to be related to differences in tree species compositions from previous studies (Hartshorn & Peralta, 1988; Lieberman et al., 1985; Lieberman et al., 1996; Web & Peralta, 1998; Clark et al., 1999). Topographic wetness index (TWI) was derived from the DEM with the SINMAP extension (Canadian Forest Products Ltd.) in ArcView 3.3 (ESRI, 2002) for estimating topographic conditions related to water catchments and high moisture conditions (Moore et al., 1991; Gessler et al., 1995). TWI is similar to TOP-MODEL developed by Beven and Kirkby (1979) for modeling hydrologic conditions important to vegetation (Miller & Franklin, 2002; Franklin, 2003). Percent slope was also included as a topographic feature related to soil drainage which is expected to influence vegetation, particularly for swamp species compositions associated with low topography (Lieberman et al., 1985; Webb & Peralta, 1998). Agricultural production systems were also expected to be related to topographic and environmental differences.

We anticipated that climate variables would be important to predicting forest composition as they are the principal factors for a number of world vegetation classification systems (Blasco et al., 2000) and for Costa Rica (Holdridge, 1967). We used WorldClim bioclimatic variables derived from monthly temperature and precipitation surfaces that are designed for ecological niche modeling over large areas (http://www.worldclim.org/bioclim.htm) (Table 2). WorldClim data incorporates SRTM elevations scaled to ~1km grid cell sizes data as an independent variable for interpolation, improving the accuracy and spatial resolution of global climate data (Hijmans et al., 2005). WorldClim bioclimatic variables capture a number of annual and inter-annual temperature and precipitation differences that have been related to biogeochemical cycles and factors effecting forest composition across environmental gradients for tropical regions (Holdridge et al., 1971; Grubb, 1977; Marrs et al., 1988; Pyke et al., 2001; Chust et al., 2006).

The amount and duration of solar radiation in a given area drives plant photorespiration and has been related to differing vegetation compositions at northern latitudes (Miller & Franklin, 2002; Pocewicz et al., 2004). Mountain environments in the study area are comprised of complex solar radiation conditions that vary with elevation (Luvall et al., 1990) and topography. Monthly diffuse solar radiation for uniform overcast sky conditions is derived using elevation data with the Solar Analyst v. 1.0 extension (Helios Environmental Modeling Institute, Lawrence, Kansas) in ArcView 3.3. Solar Analyst calculates the amount of diffuse solar radiation received by the ground or 90m grid cell in Watt·hours·m^{-2} per month from a hemispherical sky view that varies with adjacent topography. For radiation calculations, we use a hemispherical radius of 3.6 km (40 grid cells) to account for surrounding mountain terrain found at higher elevations. Potential evapotranspiration for humid areas is calculated from monthly diffuse solar radiation values and temperature surfaces following Turc (1963). Estimated values showed evapotranspiration patterns comparable to those for rainforest canopies reported by Luvall et al. (1990). We use minimum and maximum monthly values for diffuse solar radiation, solar duration and evapotranspiration as variables to be tested with DT models (Table 2).

5.3 Variable selection with Random Forest trees

Any number of variables can be added with DT model runs because variables poorly related to response categories will be left unused (Breiman et al., 1984). However, importance metrics are informative to identify principal ecological relationships between predictor variables and alliance categories, and to eliminate spatial variables that add little information, but increase computing time. We estimate each variable's importance from 1000 *Random Forest* trees using the mean decrease in accuracy when permuted and the number of times a variable is selected over another (Breiman, 2001). Input data were from 144 georeferenced forest plots described above, in addition to pixels from eleven palm swamps and twelve forest areas in the Qp and Dg alliance categories (n = 167). Training locations for *Dialium guianense* and *Qualea paraensis* alliances are obtained from additional forest inventories that were mapped over Costa Rica's digital 1:50,000 topographic sheets with tree species data in the northwestern portion of the study area as there were few plots for these categories. For *Random Forest* model runs, each of the 167 labeled plots (i.e., training samples) were attributed by all 35 of the variables (i.e., predictors) from spatially referenced grids. A reduced set of important variables was selected for landcover classification comparisons using all categories with *QUEST* and *CRUISE* models.

In addition to importance metrics, covariance measures were included to indicate potentially redundant predictor variables. Modified t-tests were used as a diagnostic test to determine correlation among the predictor variables themselves (Clifford et al., 1989). Pearson's correlation coefficients and adjusted p-values were used following the "CRH" procedure by Clifford et al. (1989), correcting for spatial autocorrelation among plot locations by adjusting the effect size via Moran's I coefficients. The PASSAGE statistics package v. 1.1 was used for correlations comparisons (Rosenburg, 2001). Highly significant covariance patterns (p <0.001) were used to eliminate spatial variables that are likely to provide similar information to DT models.

5.4 DT comparisons

Supervised classifications with *QUEST* and *CRUISE* DTs were implemented using the Rulegen extension v. 1.02 in ENVI v. 4.1(RSI, 2004) with identical training data and predictor variables selected with the procedures described above. A set of stacked grids representing predictors was divided into four square tiles ~2,000 km^2 in size to enhance computing speeds. We refer to each tile by its intermediate cardinal direction (e.g., NE, SE, NW, and SW) for discussion purposes. Decreasing the size of images reduced the number of categories present in each tile (~20) and produced smaller trees avoiding technical problems (e.g., large trees exceeded computation capacity).

For consistency with DT runs, unbiased statistical tests for variable selection and a LDA for split-point selection are applied to each tile. Class prior probabilities are modified based on input training sample size for each category, scaled from 0 to 1. Ten-fold cross-validation sample pruning and a one standard error rule were applied for pruning to reduce the size of trees with a minimum node size of five training samples. Error matrices generated from cross validation (CV) were summarized for each of the image tiles to compare CV accuracies for *QUEST* and *CRUISE* classifiers. Overall and percent user's and producer's accuracy for each category were used for comparisons to assess each model (cf. Congalton & Green, 1999).

To determine the effect of smaller image tiles on classification accuracy, we used a random selection of 1,000 pixels from each of the 32 landcover types from all four tiles. All of the data for categories with less than 1,000 training pixels were used, dividing each set into 70% of the pixels used for training (~700 pixels per class) and 30% (~300 pixels per class) set aside for predicting class membership of pixels left out of the training process (i.e., test set data). Test pixels were run with each tree to determine percent accuracy for *QUEST* and *CRUISE* classifiers. Overall percent accuracies from the test set data were compared for each DT method using unbiased variable selection, but also running *QUEST* with an exhaustive variable split-point selection similar to a *CART* procedure (Breiman et al., 1984).

5.6 Landcover changes

For conservation monitoring in the study area, we evaluated the repeatability of DT procedures for comparing differences for alliance and life zone categories between years 1986 and 2001. Separate classification trees were generated for equivalent 1986 image tiles. Classification procedures were repeated by transferring training sites for vegetation alliance categories to the 1986 image. New training sites were selected for other landcover categories located using aerial photos from years 1986/7 to 1992. Historical vegetation data and regional studies are discussed for comparison with categories mapped using DT classifiers. Summarized data for all categories are used to discuss land change trends important to the CBD and corridor objectives to maintain floristic types and connectivity between protected areas.

6. Results and discussion

6.1 Variable importance

Importance measures from 1000 *Random Forest* trees were obtained from separate runs with 7 spectral and 28 spatial variables for classifying forest alliance categories, including palm swamps. Each set of trees resulted in OOB error estimates of 46% for spectral and 19% for spatial variables, indicating the relative importance of environmental factors for prediction. *Random Forest* OOB error rates with spectral data suggest that both environmental factors and spectral bands are necessary for accurate classifications for these categories.

Importance plots from *Random Forest* runs demonstrate that TM bands 1, 5, 7 and NDVI are the principal predictor variables for alliance categories (Figure 2a). TM 5 and 7 are sensitive to plant moisture and these results were comparable to significant correlations reported for lowland Amazonian rain forest by Tuomisto et al. (2003b, c). Our results differ from Tuomisto et al. (2003b, c) with respect to TM 1 and NDVI which are important to higher elevation alliance categories in this landscape. High canopy density and compact tree crowns for upper premontane forest (Hartshorn & Peralta, 1988) likely contribute to decreased reflectance for TM 1 and increased NDVI values relative to lowland types. All but bands 3 and 4 showed at least one high value for an individual alliance category indicating that spectral characteristics differ between alliance categories. The near-infrared (TM 4) showed low importance to accuracy (Figure 2a) for closed canopy forest alliances, although it was frequently used (Figure 2b). TM 4 was considered important for discriminating crop types and secondary forest structural conditions from results of other tropical studies (Steininger, 2000; Lu et al., 2003).

Elevation is the main spatial variable contributing to reduced error rates and was selected for use with *QUEST* and *CRUISE* (Figure 3a, b). Changes in precipitation and temperature between the lowlands and foothills were important to forest composition differences as noted in other studies (Marrs et al. 1988; Lieberman et al., 1996). Marrs et al.

(1988) and Grieve et al. (1990) demonstrate that increased altitude corresponds to a near linear decrease in soil clay and increased sand and organic content affecting drainage and nutrient mineralization rates in this landscape. Elevation differences have also been show to improve markedly classifications accuracies for Amazonian rain forest types associated with terrain features (Salovaara et al., 2005).

Precipitation seasonality is the second most important factor to classification accuracy, expressed as either minimum monthly precipitation ($P14$) or coefficients of variation of monthly rainfall ($P15$) from the WorldClim dataset (Figure 3a). Monthly precipitation averaging ≤80 mm during one or two months of the year is important to individual alliance categories Qp and Dg in the western portion of the study landscape. Precipitation data obtained from weather stations located along the San Carlos and San Juan Rivers confirmed seasonally lower rainfall patterns observed from the WoldClim data. A change in species composition occurs following a precipitation gradient in the lowland portion of this landscape similar to that reported in forests across these gradients for the Panama Canal watershed (Pyke et al., 2001; Chust et al., 2006). A decrease in rainfall with distance from the Caribbean coast and its effect on vegetation changes in this landscape, in addition topographic effects, are also noted by Hammel et al. (2004).

Temperature variables associated with wet and warm periods (e.g., $T8$ and $T10$) or seasonality and cold periods (e.g., $T4$ and $T6$) are also important to accuracy (Figure 3a, b). However, no temperature variables were included with *QUEST* and *CRUISE* model runs as most were highly correlated with plot elevations ($r \leq -0.60$, $p < 0.001$). Temperature variables that did not show a significant correlation with elevation were of lower importance to accuracy (e.g., $T2$, $T3$ and $T\,7$). None of the WorldClim precipitation variables show significant correlation with plot elevations ($r = -0.31$ to 0.38, $p > 0.05$). Complex precipitation patterns between the lowland areas and Central Mountain Range likely reduced covariance with elevation at this scale. Annual precipitation declines gradually with distance from the Caribbean Costa, but increases again towards that Central Mountains.

Geographic distance has been shown to be an important predictor with spatial models for tropical forest types in Panama (Chust et al., 2006). We obtain the same OOB error rate (19%) as all other spatial variables combined using x and y coordinates from each plot to approximate geographic distance as a single predictor. No further decrease in error rates was obtained when adding coordinates with other spatial variables for *Random Forest* runs, which remained at 19%. For palm swamps, *Random Forest* model runs identified elevation and percent slope, over coordinates, as most important to accurate classifications. Adding coordinates increased error for palm swamps by 10% owing to confusion with other lowland alliance categories (e.g., Pp and Qp), though accuracy improved slightly for other categories. Distance will likely capture a number of spatially dependent environmental processes or grouped patterns in the training data (Franklin, 1998). A distance variable generated some additional error for class samples with patchy or irregular distribution patterns related to local terrain conditions. No distance variable was applied for *QUEST* and *CRUISE* model runs.

Terrain features show lower mean importance than other variables, including slope and TWI (Figure 3a), though slope is important and is an often used variable (Figure 3b) in the case of palm swamps. Topographic variation and soil properties are reported to influence significantly vegetation composition from previous studies in this area (Lieberman et al., 1985; Clark et al., 1999; Hammel et al., 2004; Jones et al., 2006). Percent slope and TWI were derived from a 90-m DEM that is less sensitive to local hillslope variation in topographic features. SRTM elevations from C-band Synthetic Aperture Radar are also estimated to have a 16-m mean vertical offset from the ground for closed canopy rain forests at the La Selva Biological Station, centered in the study area (Hofton et al., 2006). On the other hand, slope differences appear important to wetland alliance categories typical of topographic depressions. Hydrologic models estimating surface run-off or soil saturation are likely to show a stronger relationship with floristic alliances should higher resolution data of surface topography become available (Rodhe & Seibert, 1999). Solar radiation, potential evapotranspiration and duration values are likely of lower importance as modeled values follow regular elevation changes into the Central Mountains in areas where training samples were located (*also see*, Luvall et al., 1990).

A total of 12 predictor variables were used for *QUEST* and *CRUISE* model runs. Seven were spectral variables in addition to two main spatial variables, elevation and minimum monthly precipitation. Slope, TWI and solar radiation (maximum monthly diffuse radiation) were retained though their importance was low for classifying most alliance categories. These variables are expected to enhance classifications for other montane and lowland vegetation, but could be excluded depending on *QUEST* and *CRUISE* outcomes.

6.2 DT comparisons

Supervised classifications for all 32 landcover categories (Table 1) and selected variables resulted in an overall cross-validation accuracy of 93%±7.0% and 83%±15.0% for *QUEST* and *CRUISE* respectively (Table 3). *QUEST* showed favorable user's and producer's accuracy (>80%) for all but riparian forests (68%user's/78% prod.) and higher accuracy for individual categories than *CRUISE*. A number of modifications are possible to improve *CRUISE* runs, though *QUEST* performed better than expected running it in a standard unbiased mode. Variability within regrowth and other forest structural categories has traditionally limited detailed remote sensing classifications for these conditions in Central America (Castro et al., 2003). Our results indicate adequate accuracy (≥80%) for reforestation and regrowth areas (Table 3) although secondary forest >20 years old is rare in this landscape. Forest regrowth is mainly small patches of predominantly young successional areas of charral and secondary forest. Riparian forests have mixed structural conditions of remnant overstory and regenerating vegetation in wet areas that likely increase misclassification. However, narrow riparian forests are the most abundant forest cover remaining for parts of the landscape and represent potential sites for tree regeneration and seed-dispersal. Forest types grouped as structural and disturbance categories represent a large amount of the total landcover (24%) for the Costa Rica portion of the study area (80%) in 2001 (Table 3). Most of the Nicaraguan portion of the study area (20%) is inside a protected biological reserve with no signs of large disturbances. Land change trends within these categories are important for observing forest recovery patterns for biodiversity and other conservation objectives (Castro et al., 2003).

Vegetation alliance categories demonstrate higher accuracy with *QUEST* (Table 3), but more than might be expected with test set data from separate and disjoint validation samples (Ham et al., 2006). All ground information combined with higher resolution images is needed for developing high quality training data. Nevertheless, mapped alliance categories are visually comparable to historical maps and other published vegetation studies from the study area (Sandner & Nuhn, 1966; Nuhn & Pérez, 1967; Hartshorn & Peralta, 1988; Webb & Peralta, 1998; Lieberman et al., 1996; Hammel et al., 2004). *QUEST* accuracies are also similar to statistics reported by Pedorni (2003) with 89% overall accuracy for 33 landcover types covering much of our study area. Improved accuracies were obtained by Pedroni

(2003) using a maximum likelihood classifier and adjusted class prior probabilities incorporating other spatial information for classifying forest structural and life zone categories from a 1996 Landsat TM image. Prior probabilities used by us with *QUEST* and *CRUISE* classifiers were adjusted according to training sample size, though this potentially reduces accuracy for some categories with limited training information (McIver & Friedl, 2002).

Image tiles were used to reduce computing time, but likely improved classification accuracy. To estimate *QUEST* and *CRUISE* classifier accuracy for the entire study area, a random selection of training and test set pixels were taken from all four 2001 tiles for model runs. Comparisons with the randomized data assumed equal priors for all forest categories as the same number of training samples were used. Test data, left out of the training sample, classified by each model showed *QUEST* produced higher overall accuracy (81%) than *CRUISE* (77%) using the same 12 predictor variables. We saw little change in accuracy for agricultural categories, which remained >80% with the exception of fruit tree orchards (~76%). Accuracy within forest structural types decreased more substantially than for alliance categories with the exception palm swamps (Figure 4). Greater error for generic structural categories was likely produced by large differences in tree species composition between lowland and montane environments. Running *QUEST* with exhaustive split-point selection, similar to a *CART* model, showed improved overall accuracy (85%) for most forest categories, but lower than with image tiles (Figure 4). Further modifications such as an exhaustive variable selection and techniques to adjust class priors can potentially improve DT classifiers for large-area applications (McIver & Friedl, 2002; Friedl et al., 2002), but add additional training time and data constraints.

We developed no strategy to subset the four square image tiles. However, they roughly divided the foothills of Central Mountains from the lowest elevations and divided the eastern and western half of the study area. Landscape and biophysical heterogeneity was reduced by image subsets though each 2,000 km^2 area contained 20 landcover categories on average and became increasingly patchy over time (Figures 5a - d). Supervised classifications with *QUEST* and the image tiles produced accurate and detailed landcover data that is frequently missing for priority conservation areas such as the present corridor study area.

6.4 Landcover comparisons

This research was conducted under the premise that a habitat monitoring procedure useful for CBD and other conservation objectives must be repeatable. The *QUEST* classifier used with each tile produced favorable results in terms of both speed and accuracy and was used again for classifying landscover from a 1986 Landsat TM image. Cross-validation accuracy results showed 96% for all image tiles from 1986 using *QUEST* that is consistent with accuracy from 2001 tiles. Higher accuracy for 1986 can be attributed to fewer crops and forest structural types that produced some lower accuracy with the 2001 image date (Figures 6a, b). Tree plantations and secondary forest were nearly absent from the study landscape in 1986.

QUEST classifications for 1986 and 2001 resulted in similarly defined floristic alliances, though categories did not always overlap. Swamp forests and the Pc alliance in Figure 5a reveal somewhat different spatial patterns between image dates. A greater amount of ground water present for the 1986 image date likely aided discriminating swamp forests from the Pc alliance. Other artifacts are attributed to some differences in the training data used for 2001 and increasingly heterogeneous landscape conditions. “Fuzzy” boundaries between alliance categories precluded direct post-classification change comparisons via classified pixels for the two image dates. However, area estimates for each category and visual differences over time were informative for detailed landcover monitoring (Figures 5a - d). Spatial and temporal patterns for mapped categories are discussed with respect to historical and regional vegetation studies.

Spatial patterns of mapped forest alliance categories in the foothills of the Central Mountains are similar to life zones and show strong transition with elevation (Figure 5a). A break between lowland species compositions is evident from plots with a near absence of the abundant tree species *Pentaclethra macroloba* above ~300 m elevation. Reoccurring dominant trees noted by Hartshorn and Peralta (1988) are evident from our plots above the break with lowland *P. macroloba*. Forest with a notable increase in *Tapirira guianensis* and *Dendrobangia boliviana* (Ta alliance), and other species with increased elevation, confirm forest composition patterns indicated by Lieberman et al. (1996). Strong elevation patterns from training areas sampled on the ground for these environments lend themselves to floristic categories analogous to life zones to some extent. Forest area in the foothills and higher elevation alliance categories decreased over time, but had greater area inside national park boundaries as compared to lowland vegetation alliances (Figure 7). Country-wide forest change studies using Landsat TM data by Sánchez-Azofiefa et al., (2003) show that most forest changes occur outside protected areas between 1986 and 1997 for this location (e.g., Braulio Carrillo National Park). We observe secondary forest recovery for previously disturbed forests mainly inside Braulio Carrillo; that is the main body of forest in Figure 5a.

Vegetation alliances mapped in the lowlands were visually analogous to forest associations mapped by Nuhn and Pérez (1967), also using canopy tree species, and plots described by Sandner and Nuhn (1966). Particularly notable are categories dominated by *P. macroloba* (Pc) or *Dialum guianense* (Dg) located in NE and NW image tiles, respectively. *P. macroloba* and *D. guianense* also form mixed stands on flat terrain close to the San Carlos River observed from plots measured by Sandner and Nuhn (1966) and our plots sampled from nearby locations. *QUEST* classifications become mixed between the Dg and Pc alliances in these transitional areas (Figure 5c) that were related to precipitation seasonality from *Random Forest* model runs. The Pc alliance type was more extensive in the northeastern part of the study area (Figure 5b) and coincided with extensive *P. macroloba* and *C. guianese* forest mapped by Nuhn and Pérez (1967). As much as 60% of the basal area of forest canopy trees is dominated by these two species, from our plots, similar to forests described by Webb and Peralta (1998). We distinguish the Pc type from swamp forest as an only occasionally flooded type with a lower abundance of species common to more frequently inundated sites (Lieberman et al., 1985; Webb & Peralta, 1998). The Dg alliance appears highly fragmented although the most recent forest loss has occurred in the Pc type (Figure 5b and 7). Most of the Pc type is outside protected areas with only as small proportion inside of the La Selva Biological Station protected area (Figure 7). Agricultural systems surrounding many of the most isolated forest areas (e.g., Dg) have become increasingly intensified shifting from pastures to crop types that are typically without tree cover (summarized in Figure 6b).

Forest composition differences in the study area with increased precipitation seasonality were comparable to trends observed across the Panamanian isthmus (Pyke et al., 2001) mapped by Chust et al. (2006). Increased dominance by tree species in the Vochysiaceae family (Qp alliance) shows a transition in forest composition from *P.*

macroloba dominated forests in the lowlands. Seasonally lower precipitation is an important variable for accurate classification of the Qp alliance type, but is also well separated from *P. macroloba* forest via mid-infrared spectral bands (Sesnie et al., in review). Much higher tree species diversity has been reported for the Qp type from botanical collections relative to *P. macroloba* dominated forests in the lowlands (Hammel et al., 2004). The Qp forest alliance appears to increase in 2001 because of high cloud cover obscuring forest in this area for 1986 (Figure 7). These forests have been isolated from agricultural development for complex reasons. In general, human migration and settlement along foothills of the Central Mountains (Sandner & Nuhn, 1966) and later border activities during the Contra wars (Girot & Nietshmann, 1992) delayed colonization of these areas.

QUEST classified wetlands overlap spatially with Costa Rica's IUCN categories (Figure 5b) mapped from 1:200,000 topographic (Digital Atlas of Costa Rica, 2004) although vegetation attributes from these maps are highly generalized. Our wetland alliance types show greater agreement with Costa Rica's 1:50,000 topographic sheets that correspond with locations we recorded in the field and 1:60,000 maps by Nuhn and Pérez (1967). Several tropical studies have shown that swamplands can be accurately mapped using Landsat TM bands (Foody & Hill, 1996; Lobo & Gullison, 1998; Pedroni, 2003). However, with this study we found that lowland *P. macroloba* forests and other types (e.g., Qp) are sometimes difficult to discriminate from small patches of swamp vegetation without the use of SRTM elevation data. The *Raphia taedigera* palm forms monospecif stands in swamps, but occasionally develop mixed compositions with other broadleaf species (Urquhart, 1999). Salovaara et al. (2005) also show that combining Landsat TM bands with SRTM elevation data is necessary for classifying Amazonian forest types related to lowland terrain features. Wetlands are generally protected within less restrictive wildlife refuge and special wetland status, but show deceased area over time with the exception of herbaceous swamps (Figure 7). Herbaceous swamps are rare and often cover small areas in this landscape, with the exception of a single large area used as a training site.

Summarized landcover data from the *QUEST* classifier show large changes in the study area for both the agricultural sector and forestry development (Figure 6a, b). The extent of urban centers has also more than doubled in the study area since 1986 indicating rapid economic development (Figure 6c). We determine that 61% of the Costa Rican portion of the study area is in some kind of forest cover or natural habitat (Table 3), most of which is concentrated in national parks and the SJ-LS corridor. Agricultural changes between image dates show a large-scale shift from cattle ranching to more intensively managed export crops, but also to forest enterprises (Table 3, Figure 6a, b). Intensively managed land for fruit and tree crops have doubled or become a new feature in the landscape (e.g., reforestation). Forest cover has mainly increased in the form of tree plantations and secondary forest to a lesser degree (Figure 6a). National programs to establish and manage tree plantations (Watson et al., 1998) have had a large impact on landscape composition in the study area. Natural regeneration and replanted areas present forest management opportunities for habitat restoration important to corridor objectives and connectivity (Lamb et al. 2005). We achieve the lowest classification accuracy for riparian forest remnants areas though these forest remnants appear to be an increasingly important source of native forest cover on the landscape (Figure 6a).

Landcover differences detected with the *QUEST* classifier significantly improved information on the extent of floristically based alliance categories. Habitat losses between 1986 and 2001 for specific alliance categories are observed in the foothills, though higher losses occurred for lowland categories on level terrain (*also see* Sader & Joyce, 1988). Overall, natural habitats decreased by 16% and became interspersed with increasingly intensified agricultural land use (Figure 6a). A present focus of Costa Rican conservation programs is to prevent further natural forest losses and to retain environmental services by paid forest protection contracts with landowners (Snider et al., 2003). Remaining Dg and Pc lowland alliance categories mapped with *QUEST*, mainly inside of the SJ-LS Corridor, are considered areas vulnerable to land conversion that could benefit from private protection.

7. Conclusions

DT classifiers used with this study are well suited for integrating Earth observation data to produce accurate and repeatable classifications. Forest composition and derived alliance categories showed a strong relationship to the physical environment in this landscape. Climate and SRTM elevation data are important to accurate classification of alliance categories as are TM spectral bands. The Landsat TM sensor provided an essential archive of multispectral data for monitoring past and present landcover conditions. Complex relationships between predictor variables and alliance categories are further elucidated using multi-classifier and multivariate DT models for both variable selection and enhanced landcover classification.

Of the techniques examined, the *QUEST* classifier is the most efficient and accurate method to integrate Landsat TM bands with other geospatial data. Image sub-setting improves accuracy by reducing landcover heterogeneity across a large geographic area. These procedures show capabilities to enhance habitat mapping and monitoring complementary to multiple conservation objectives where retaining floristic diversity and recruiting of new forest cover are conservation objectives. Much of the remaining forest and wetland types outside parks in this study area are within a recognized conservation corridor that is privately owned. Vegetation alliances and agricultural areas have undergone a dramatic transformation in the 15-year time period indicating intensified land use throughout the study area. The SJ-LS Corridor and others like it are presently the focus of national programs to retain remaining natural forest on private land. Area comparison for alliance categories provided adequate information for targeting conservation activities in native habitats vulnerable to change or areas of special conservation interest. Continued monitoring of land use changes of remnant and recovering vegetation as well as surrounding landscape features will be essential to meeting CBD and corridor goals for retaining viable habitats for biodiversity from our observations. Programs to promote reforestation and natural regeneration for restoration, carbon sequestration and watershed protection objectives will also require more detailed land cover data to monitor their outcomes.

Available imagery and important relationships between vegetation and the biophysical environment are expected to change from location to location. Our results suggest a framework for testing and incorporating variables with DT classifiers that are broadly applicable to priority conservation areas. The methods tested here can be readily implemented using supervised classification techniques familiar to individuals with moderate technical experience. Although a large amount of ground and other data were collected to implement this approach, we found that there are many existing data resources to aid detailed classifications for human dominated landscapes. Use of expert knowledge or other available information and added procedures to automate some aspects of DT classifications could quickly improve landcover mapping and monitoring to meet CBD and other conservation goals in these complex environments.

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Tables

Table 1. Forest and landcover categories used with DT classifiers. The number of training pixels the total number used for DT classifiers from all four 2000 km^2 image tiles. Forest and wetland alliances marked with an asterisk (*) were used with *Random Forest* trees to generate variable importance metrics.

Abbrev.	Categories	Training pixels	Source
Forest & wetland floristic alliances, Holdridge Life Zones			
Pc*	*Pentaclethra macroloba, Carapa guianense, Welfia georgii*	6519	Plots/Inv.
Pp*	*P. macroloba*/arborescent palm spp.	6948	Plots/Inv.
Dg*	*Dialium guianense, Brosimum alicastrum, Sclerolobium costaricense*	1680	Plots/Inv.
Qp*	*Qualea paraensis, Dipteryx panamensis, Vochysia ferruginea, Couma macrocarpa,*/ arborescent palm spp.	2786	Plots/Inv.
Ta*	*Tapirira guianensis, Dendrobangia boliviana/*arborescent palm spp.	1685	Plots
Va*	*V. allenii/Macrohasseltia macroterantha*	2146	Plots
Cy*	*Cyathea spp*., *Guarea spp.*	2211	Plots
bmh-mb	Lower montane forest	4475	Photo/map
bmh-p	Pre-montane rain forest	425	Photo/map
bp-m	Montane forest	96	Photo/map
Ps*	Palm swamp - *Rafia taedigera* dominated swamp	1264	Photo/GPS
Sf	Forested swamp - inundated forest *Pterocarpus officinales*, *Simira maxonii*, *Grias cauliflora*, *P. macroloba*	1844	Photo
Hs	Herbaceous swamps and floodplains - inundated sedge grasses, caña brava (*Gynerium sp.*) and occasional trees	965	Photo/GPS
Forest structural types			
Re	Reforestation - mainly tree plantations of exotic or native tree species	6387	Photo/GPS
Ch	Charral - native regrowth dominated by shrub and herbaceous vegetation	1976	Photo/GPS
Se	Secondary forest – tree dominated forest re-growth aged ~5-20 years after agricultural abandonment	3275	Photo/GPS
Rf	Riparian forest - Mixed remnant trees and forest regrowth along waterways	1954	Photo/GPS
Agriculture & other			
Ba	Banana	1249	Photo/GPS
Hp	Heart of palm	823	Photo/GPS
Yu	Yuca (cassava)	265	Photo/GPS
Pi	Pineapple	915	Photo/GPS
Bb	Bamboo	187	Photo/GPS
Pa	Pasture	5234	Photo/GPS
Su	Sugarcane	1123	Photo/GPS
Ft	Fruit tree orchards	1181	Photo/GPS
Co	Coffee	258	Photo/GPS
Cp	Cultivated palms	144	Photo/GPS
As	Agricultural soil	1565	Photo/GPS
Wa	Water	1227	Photo/GPS
Ur	Urban	542	Photo/GPS
Ro	Rock	566	Photo/GPS
Ns	Nursery shade	239	Photo/GPS

Table 2. Image and raster data from Landsat TM, SRTM-DEM and Worldclim bioclimatic surfaces for use as predictor variables with DT landcover classifications. A numerical code was used for SRTM and WorldClim variables for variable importance plots (Figures 3).

Varibles	Abr.	Code	Units
Landsat TM/30x30m			
TM 1	b1	-	0.45 - 0.52µm
TM 2	b2	-	0.52 - 0.60
TM 3	b3	-	0.63 - 0.69
TM 4	b4	-	0.76 - 0.90
TM 5	b5	-	1.55 - 1.75
TM 7	b7	-	2.08 - 2.35
NDVI	NDVI	-	
SRTM-DEM/90x90m			
Elevation	El	1	m
Solar duration (max month)	Sdur+	2	Mean hrs daily
Solar duration (min month)	Sdur-	3	Mean hrs daily
Diffuse solar radiation (max month)	Rad+	4	$kw\cdot h\cdot m^{-2}\cdot mo^{-1}$
Diffuse solar radiation (min month)	Rad-	5	$kw\cdot h\cdot m^{-2}\cdot mo^{-1}$
Potential evap. (max month)	Pe+	6	mm/day
Potential evap. (min month)	Pe-	7	mm/day
Topographic wetness index	TWI	8	0-3 (low - high)
Percent slope	Sl	9	0-100%
WorldClim/991x991m			
Annual mean *T*	*T*1	10	°C
Mean diurnal range (Mean of monthly (max *T* - min *T*))	*T*2	11	index
Isothermality (*T*2/*T*7) (* 100)	*T*3	12	index
T seasonality (standard deviation *100)	*T*4	13	index
Max *T*of warmest month	*T*5	14	°C
Min *T* of coldest month	*T*6	15	°C
T annual range (*T*5-*T*6)	*T*7	16	°C
Mean *T* of wettest quarter	*T*8	17	°C
Mean *T* of driest quarter	*T*9	18	°C
Mean *T* of warmest quarter	*T*10	19	°C
Mean *T* of coldest quarter	*T*11	20	°C
Annual *P*	*P*12	21	mm
P of wettest month	*P*13	22	mm
P of driest month	*P*14	23	mm
P seasonality (Coefficient of Variation)	*P*15	24	CV
P of wettest quarter	*P*16	25	mm
P of driest quarter	*P*17	26	mm
P of warmest quarter	*P*18	27	mm
P of coldest quarter	*P*19	28	mm

Table 3. Overall user's and producer's percent accuracy are reported as the average from each of the four image tiles for the 2001 TM image. [1]Area estimates for each landcover category is calculated for only the Costa Rican portion of the study area (80%) from landcover data generated with the *QUEST* classifier excluding 3% cloud cover.

	QUEST		**CRUISE**			
	Overall %	92.9±7	**Overall %**	82.7±15		
Category	**prod.%**	**user%**	**prod.%**	**user%**	**[1]Area (km^2)**	**Area (%)**
Alliance/Life zone						
Pc	91	92	75	83	295	4.7
Pp	93	94	77	86	467	7.3
Dg	83	85	57	77	125	2.0
Qp	94	94	90	88	287	4.5
Ta	95	98	92	77	179	2.8
Va	98	98	83	94	156	2.5
Cy	98	99	96	93	264	4.2
bmh-mb	98	99	91	97	352	5.5
bp-m	98	98	95	98	13	0.2
bmh-p	98	100	96	98	9	0.1
Palm swamp	95	97	88	67	53	0.8
Swamp forest	95	89	79	56	92	1.4
Herb. swamp	88	90	86	70	53	0.8
						37%
Structural types						
Riparian forest	78	68	83	38	506	8.0
Reforestation	89	88	77	64	455	7.2
Charral	86	84	85	68	280	4.4
Secondary forest	86	84	80	59	281	4.4
						24%
Agriculture/other						
Banana	95	94	93	86	116	1.8
Heart of palm	94	92	89	72	51	0.8
Yuca	95	90	97	59	17	0.3
Pineapple	99	97	96	81	36	0.6
Bamboo	97	97	95	87	16	0.3
Pasture	96	97	90	97	1477	23.3
Sugar cane	98	97	91	96	154	2.4
Fruit trees	87	90	81	56	62	1.0
Coffee	97	98	90	92	61	1.0
Cultivated palms	93	95	97	75	15	0.2
Soil	99	98	97	95	143	2.3
Water	98	97	98	94	62	1.0
Urban	95	95	98	91	30	0.5
Rock	97	95	94	97	16	0.3
Nursery shade	95	99	99	98	7	0.1
						36%

Figures

Figure 1. The 8,000 km^2 study area that includes the San Juan – La Selva Biological Corridor (2,425 km^2) providing a forested connection between Costa Rican and Nicaraguan protected areas. Quarter hectare forest plots were located at a minimum distance of 300m apart and 150m from a forest edge (shown right), but were distributed in forest fragments across the study area (shown left). Plots labeled Pp = *Pentaclethra macroloba* and arborescent palm*s* alliance and Ps = palm swamps (*Raphia taedigera*) referenced with a GPS in the lowlands. Rectangles are the locations for map examples shown in Figure 5a - c.

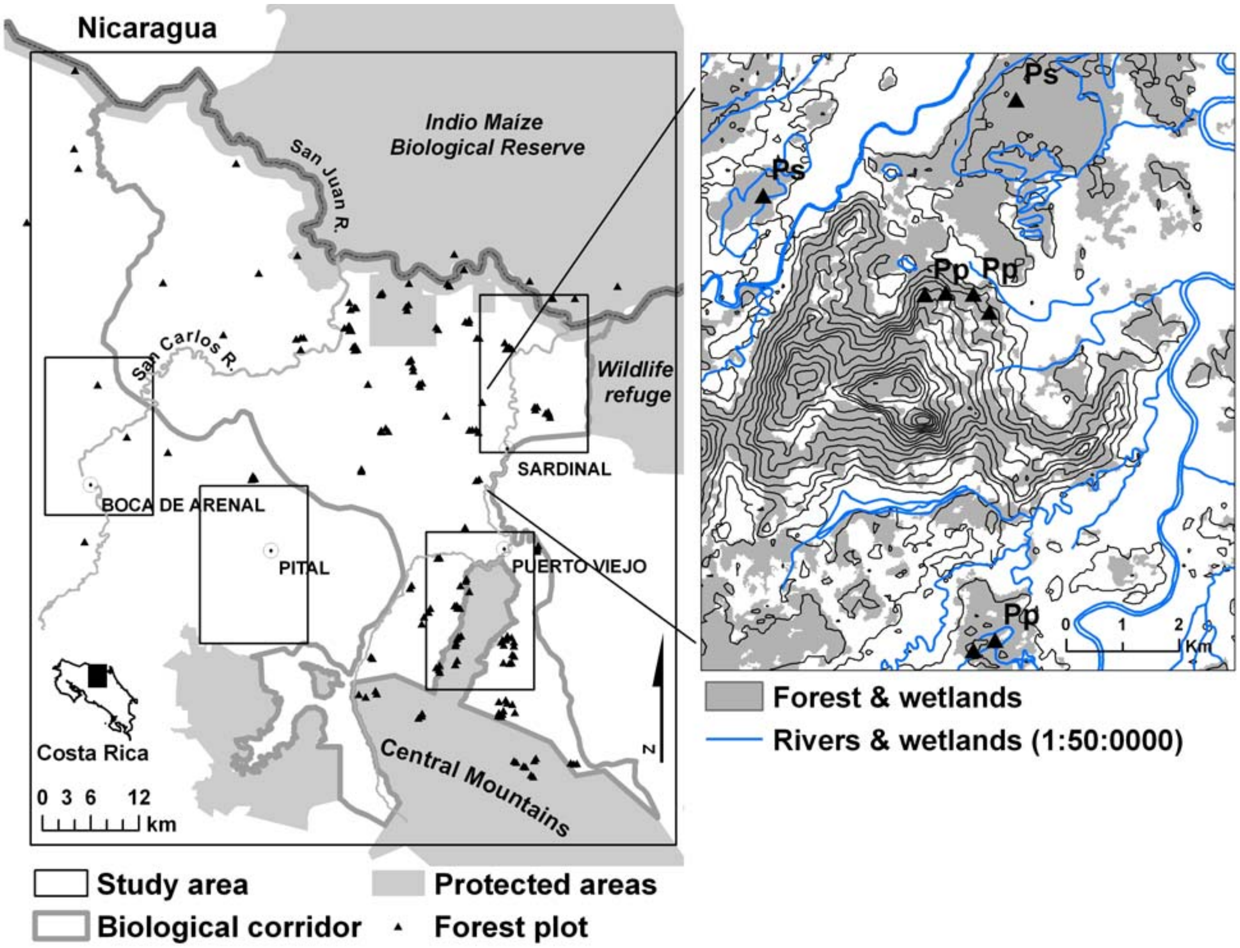


Figure 2. Variable importance plots for each TM band and NDVI from 1000 *Random Forest* trees with vegetation alliance categories. Graphs represent, a) each variables contribution to a mean decrease in accuracy from permutations and b) how often a variable was selected for node splitting from a random selection of three variables. The magnitude of mean decrease in accuracy as a variable is permuted or the number of times selected for splitting indicates its importance to accuracy for test samples left out of individual tree construction.

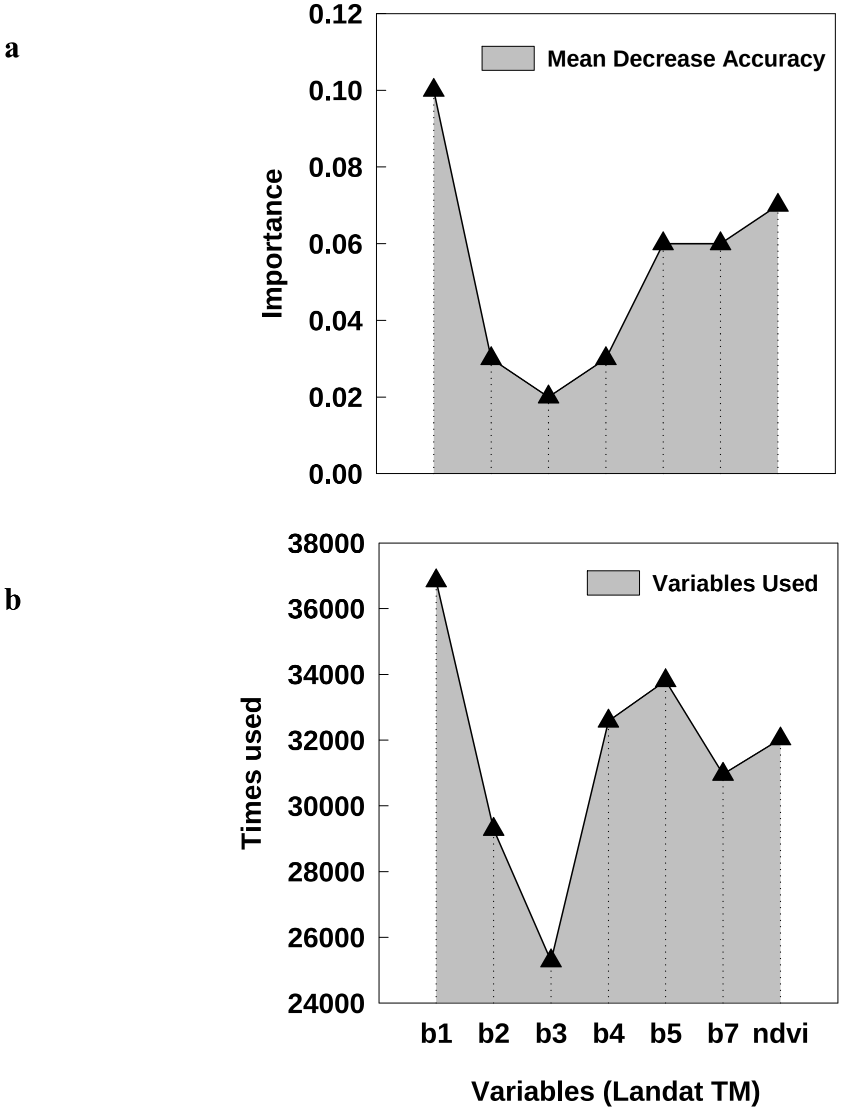


Figure 3. Variable importance plots for each of the 28 biophysical variables from SRTM-DEM and WorldClim data with 1000 *Random Forest* classification trees with vegetation alliance categories. Numbers (codes) on the x-axis are referenced in Table 2. Peaks are generally elevation (1) and temperature seasonality (13) and driest month precipitation (23) variables indicating the importance of these factors to classification accuracy.

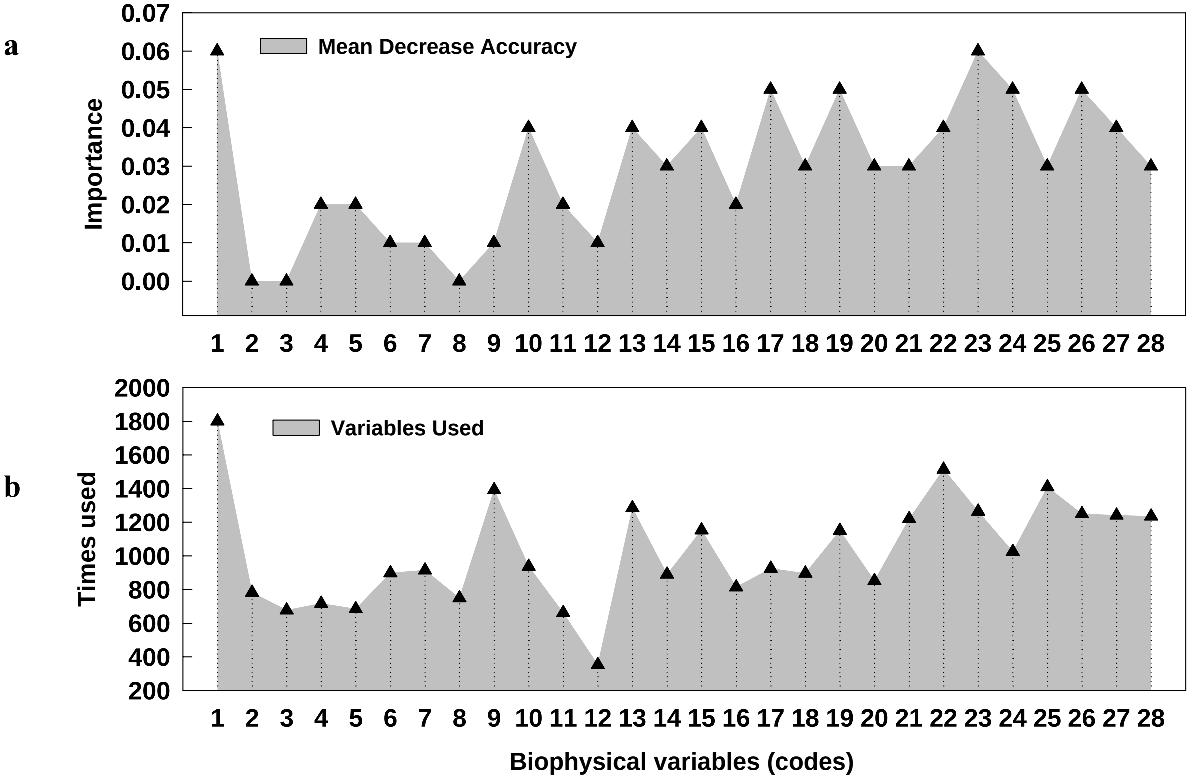


Figure 4. Decision tree results with randomized training and test set data for alliance and structural types from the 8,000 km^2 study area compared with *QUEST/Tile* cross validation accuracies from four 2,000 km^2 classified image tiles. *CRUISE* and *QUEST* were run in an unbiased mode and *QUEST/CART* was run using an exhaustive split point selection. Life zone categories are not shown.

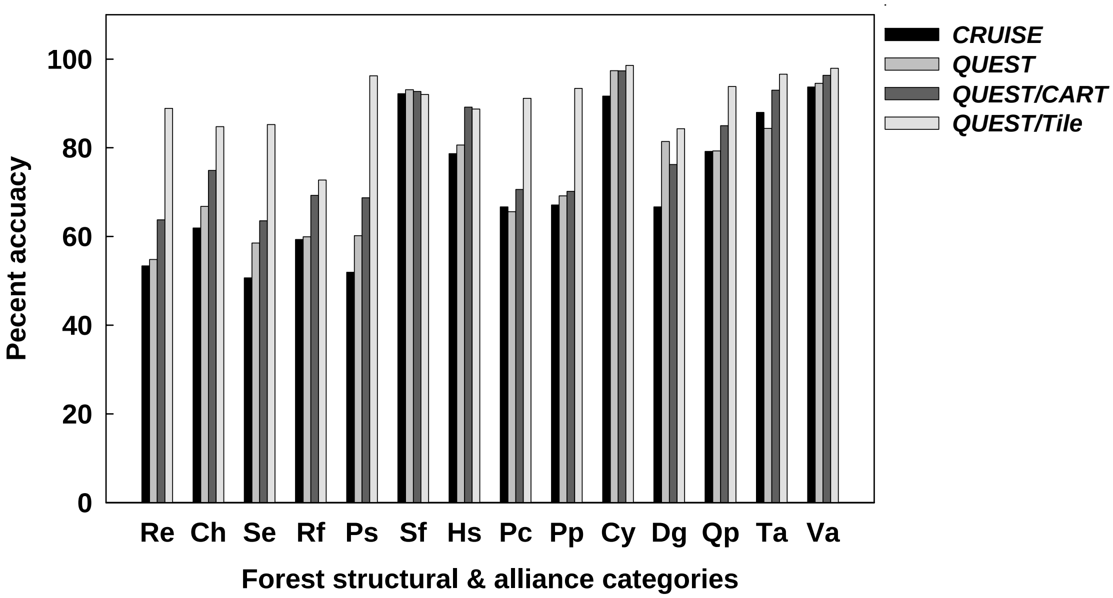
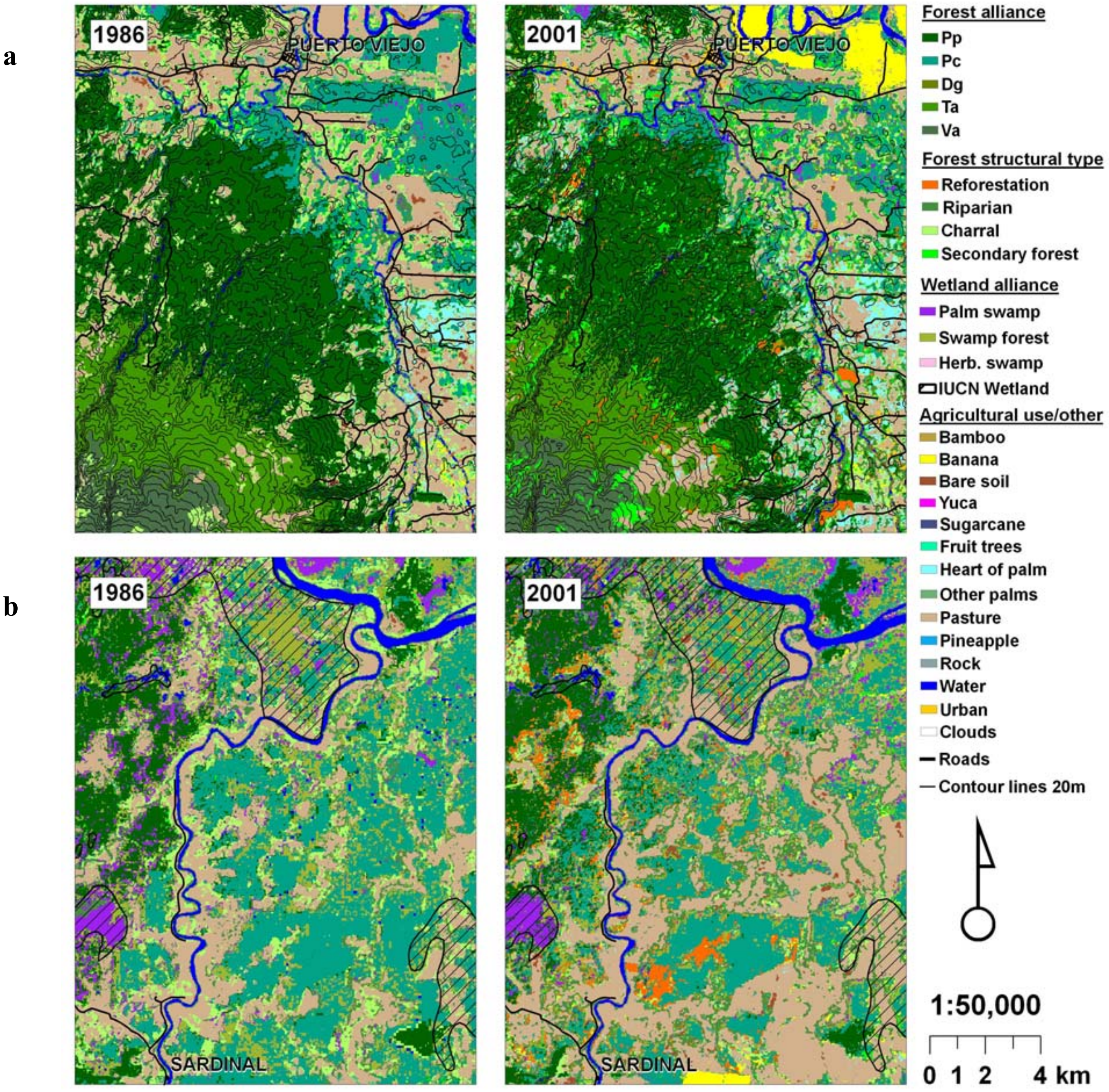


Figure 5. Landcover types classified using *QUEST* and TM images from 1986 and 2001. Paired maps reading left to right are; a) forest alliance categories for the foothills of the Central Mountains, b) lowland forest and wetlands fragmentation inside the SJ-LS Corridor, c) transition area between Pc and Dg forest types near the San Carlos River, and d) land use change surrounding isolated forest remnants. The location of landcover example areas are shown in Figure 1.



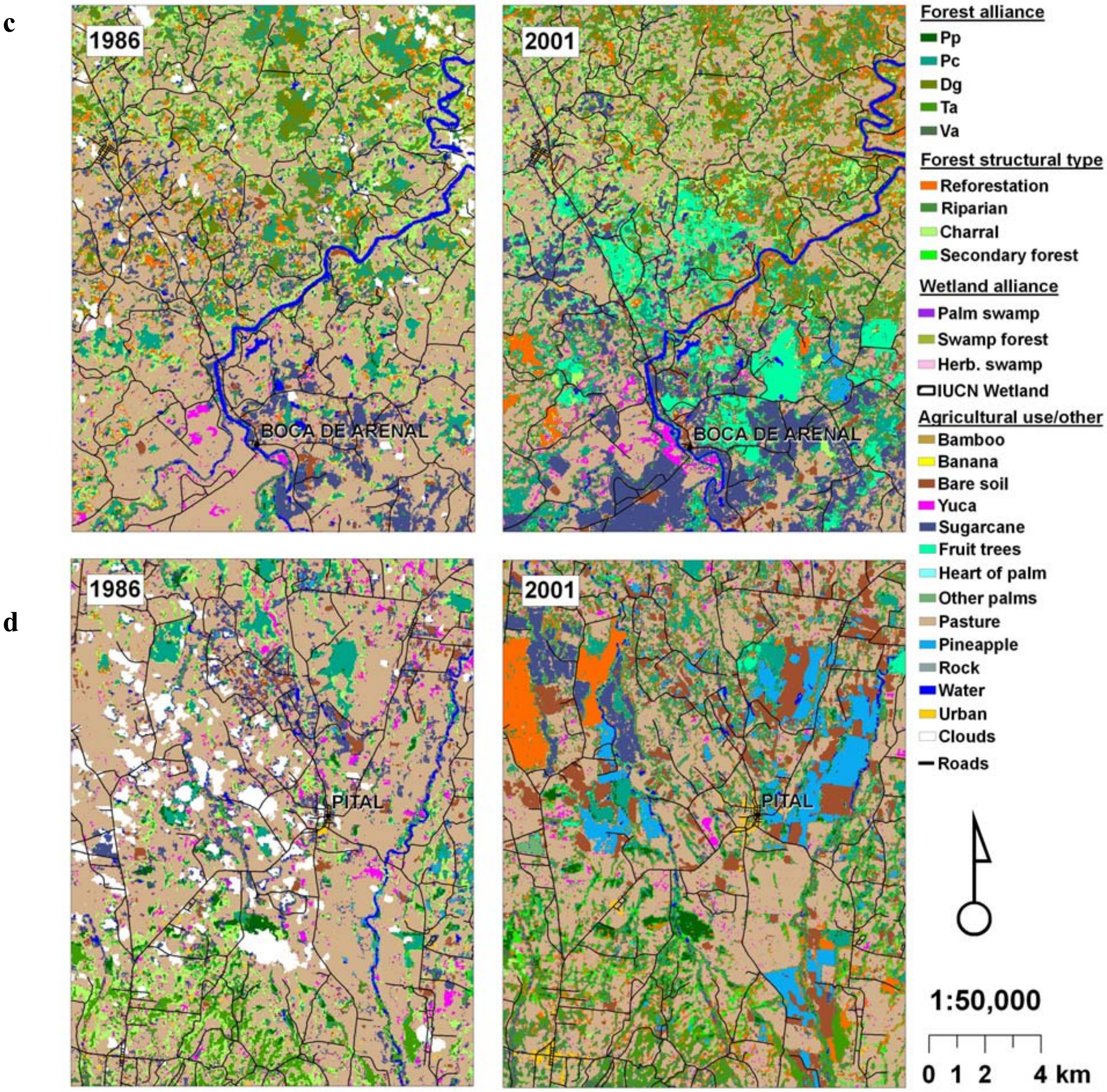

c
1986
BOCA DE ARENAL
2001
BOCA DE ARENAL
d
1986
PITAL
2001
PITAL
Forest alliance
Pp
Pc
Dg
Ta
Va
Forest structural type
Reforestation
Riparian
Charral
Secondary forest
Wetland alliance
Palm swamp
Swamp forest
Herb. swamp
IUCN Wetland
Agricultural use/other
Bamboo
Banana
Bare soil
Yuca
Sugarcane
Fruit trees
Heart of palm
Other palms
Pasture
Pineapple
Rock
Water
Urban
Clouds
Roads
1:50,000
0 1 2 4 km

Figure 6. Summarized forest and landcover data for the Costa Rican portion of the study area from years 1986 and 2001. Forest and wetlands obstructed by clouds for the 1986 image date were corrected by substituting classified pixels in these categories from a 1996 Landsat TM image previously classified with *QUEST* procedures.

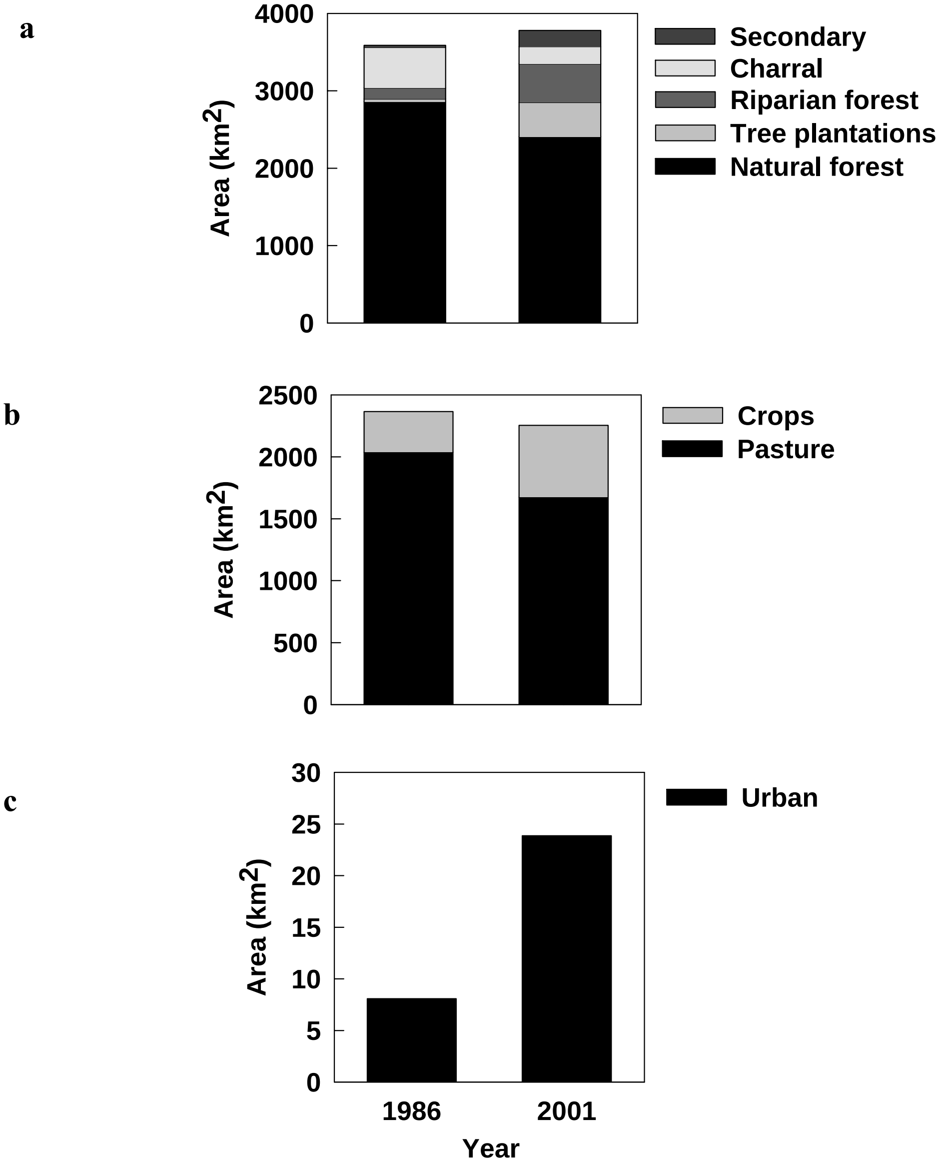
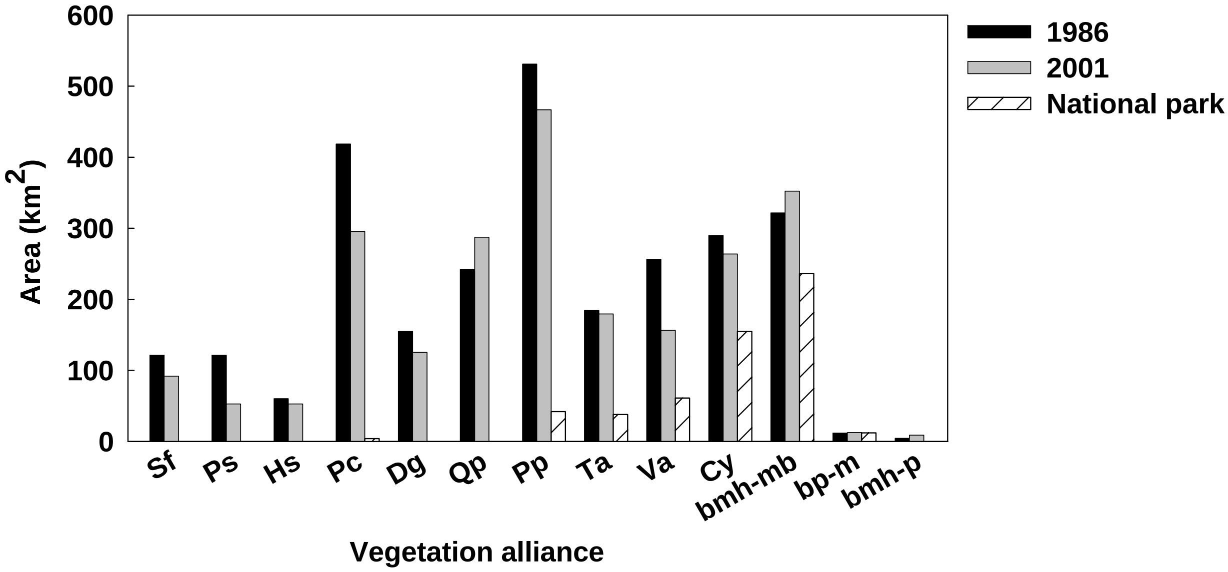


Figure 7. Areas differences for alliance and life zone categories from years 1986 and 2001. Categories are ordered from the lowlands (left) to higher elevation areas (right). Hatched bars represent the amount of forest area within a national park in 2001, but includes La Selva Biological Station property that are Pp and Pc types. Bars showing increased forest area for 2001 were obscured by clouds in 1986.



Chapter 4

Consequences of environmental service payments for forest retention and recruitment in a Costa Rican biological corridor

ABSTRACT

Compensation to landowners for forest-derived environmental services has gained international recognition as a mechanism to combat forest loss and fragmentation. This approach is widely promoted with little evidence demonstrating its prospects for encouraging forest stewardship and conservation. Costa Rica provides a compelling case study where a 1996 Forestry Law initiated environmental service payments and prohibited forest conversion to other land uses. We examined these novel policies to determine their influence on landowner decisions that affect forest change, carbon services, and connectivity in a 2,400 km^2 biological corridor. Landsat images were used to compare landcover changes before and after 1996, and these data were linked to landowner surveys investigating land use decisions. Carbon services provided by secondary forests were examined both above- and belowground. Forest change observations were corroborated by landowner survey data, indicating that environmental service payments contributed positively to forest retention and recruitment following implementation of the 1996 Forestry Law. Rates of natural forest loss declined from -1.43 to -0.20 % yr^{-1}. Forest cover and connectivity increased through tree plantations and secondary forest recruitment, but these forest types sometimes replaced natural forest prior to 1996. Secondary forest carbon storage approached values found in primary forest after 25-30 years of succession, though few landowners retained natural regeneration. Secondary forests and attendant carbon services will persist as minor landscape components without legal or financial incentives. The Costa Rican experience provides evidence that environmental service payments can be effective in retaining natural forest and recruiting tree cover when focused in biological corridors.

Keywords: biological corridor; carbon storage; Costa Rica; environmental service payments; forest change; landowner decision making; livelihoods; secondary forest

INTRODUCTION

Forest loss and fragmentation represent a global threat to biodiversity, ecosystem processes, and human welfare (Millennium Ecosystem Assessment 2005). Demands on forests and the environmental services they provide are projected to increase as development pressures reduce remaining private forests lacking protected status (Defries and others 2005). In response to these threats, incentive programs encouraging private forest stewardship have emerged, offering compensation to landowners who retain forests and associated services that might otherwise be lost to alternative land uses (Pagiola and others 2002). Direct payments to landowners to plant or protect forests are promoted as an effective mechanism for providing environmental services (Ferraro and Kiss 2002), consistent with the 1997 Kyoto Protocol and the 1992 Convention on Biological Diversity. However, the effects of these payments on forest cover and targeted environmental services remain relatively unknown.

Costa Rica presents a compelling case study to analyze an environmental service payment program (*pago por servicios ambientales*, PSA) that provides direct payments to landowners for reforestation, sustainable forest management, and natural forest protection. Reforestation incentives for private landowners to establish tree plantations were first initiated in Costa Rica following several decades of high deforestation (Watson and others 1998). During the mid-1980s, tradable bonds (CAF) and upfront payments (CAFA) became available to cover costs associated with establishing and maintaining tree plantations (Watson and others 1998). Additional incentives initiated in 1990 targeted sustainable forest management (CAFMA) and were expanded in 1995 to include forest protection. Costa Rica built on the legacy of these programs with the 1996 Forestry Law (no. 7575) that implemented four novel features including: 1) a national definition of forest, 2) prohibition of natural forest conversion to any other land use, 3) deregulation of tree plantation management, and 4) a voluntary PSA program to compensate landowners for watershed protection, biodiversity conservation, carbon sequestration, and aesthetic values.

Legal and institutional support for the PSA program is provided by the National Fund for Forest Financing (FONAFIFO), an organization designed to promote sustainable rural development among small and medium-sized landowners (Snider and others 2003). National PSA priorities have concentrated efforts in biological corridors and poorly developed regions of the country with more than US\$124 million expended on >5000 km^2 of land (FONAFIFO 2006). PSA contracts with landowners typically last for five years and payments range from ~\$220 ha^{-1} for the forest protection program to \$560 ha^{-1} for reforestation.

The objectives of 1996 Forestry Law and PSA are to provide environmental services through forest stewardship; however their impacts on carbon storage, forest structure, and connectivity in fragmented landscapes are unclear. Further, the relative influence of forest policies and programs on landowner decisions to maintain or increase forest cover remains poorly understood. Accordingly, we applied an integrated research approach to determine the extent to which the 1996 Forestry Law and PSA incentives for landowners to maintain or replant forests translate into enhanced forest conservation, carbon services, and connectivity. We studied these processes in the San Juan ─ La Selva Biological Corridor, a PSA focal area designed to retain linkages between protected areas in Costa Rica and southern Nicaragua (Figure 1).

Studies of landcover change detection, ecosystem ecology, and rural sociology were unified to address five specific questions: 1) Has the annual rate of forest loss declined substantially for private forest land in the Corridor as expected under the 1996 Forestry Law? 2) To what extent are changes in forest cover attributable to the ban on forest clearing and/or payments to protect forests? 3) Have incentives for reforestation been a major catalyst for landowners to establish tree plantations? 4) What is the outlook for recruiting forest cover via secondary succession as a potential source of valued carbon services under the 1996 Forestry Law? 5) Are PSA programs an effective conservation mechanism for retaining habitat connectivity between protected areas?

STUDY AREA

The present case study focuses on the San Juan – La Selva Biological Corridor (2,425 km^2) in northern Costa Rica where PSA contracts occur on ~22% (538 km^2) of the land area (Rojas and Chaverría 2005). A larger surrounding study area (6,349 km^2) was selected to facilitate forest land change comparisons in areas bordering the Corridor (Figure 1). The Corridor contains one of the largest aggregations of remnant forest in the region, and private forests outside of protected areas represent an important connection between formerly continuous montane and lowland forests (Butterfield 1994a). Diverse vegetation types in the Corridor cross five Holdridge Life Zones and three transitional zones given the region's varied climatic conditions along altitudinal and longitudinal gradients (Holdridge 1967).

Costa Rica passed its first Forestry Law in 1969 (no. 4465) that has since undergone several revisions. However, agricultural development and colonization programs have taken precedent over forest stewardship, leading to forest cover reductions in the country's northern region since c. 1950 (Butterfield 1994b). Colonization programs expanded roads and settlements during the 1970s to open territory to landless farmers (Butterfield 1994b), while low interest loans for cattle production and high beef prices further enhanced land colonization and conversion of forest to pasture (Schelhas 1996). Forests were used as an open access resource by colonists, contributing to rapid deforestation and highly fragmented landscape conditions (Butterfield 1994a).

A severe economic crisis at the end of the 1970s forced Costa Rica to accept monetary assistance (Montanye and others 2000) tied to a series of structural adjustment loans that led to the promotion of non-traditional export crops (e.g. pineapple, heart of palm) (De Camino and others 2000). Cattle exports dropped significantly in the early 1980s and cattle herd sizes declined after 1988 (Ibrahim and others 2000). This trend reduced pressure to clear natural forest and led to temporary abandonment of some pastures. However, many pastures were soon converted to crops or used for government land redistribution programs (Butterfield 1994b). Costa Rica continued the promotion of export crops simultaneous with conservation initiatives throughout the 1990s. Evolving development strategies continue to raise questions about how forests will fare under new policies.

METHODS

Several data integration efforts were used to address the research questions above. We compared forest retention, recruitment, and other landcover changes derived from satellite images before and after 1996 with landowner surveys to evaluate the influence of forest policy and PSA incentives on observed forest patterns. We also examined secondary forest carbon storage using plot-level data linked to landcover changes and landowner decisions regarding secondary forest establishment. Finally, we employed forest connectivity metrics as a unifying measure of forest retention and recruitment within the Corridor.

Forest and landcover change

We selected five Landsat Thematic Mapper (TM) satellite images (WRS Path 15 Row 53) with low cloud cover from years 1986, 1996/97, and 2001 to observe landcover changes before and after implementation of the 1996 Forest Law. For simplicity, we refer to the time period before the 1996 law (1986-1996) as T1 and the period afterward (1996-2001) as T2. ENVI v.4.1 image processing software (RSI 2004) was used to prepare and classify images.

All images were individually co-registered to a 1996 TM image referenced to locations on the ground for spatially accurate comparisons.

Forest and landcover categories were selected based on prior landcover information for northern Costa Rica from 1996 (Pedroni 2003). Five forest categories were used for landcover change detection analyses including: 1) natural forest (closed canopy or selectively logged old-growth forest and natural palm swamps), 2) a *charral* phase (native shrub and herbaceous regeneration), 3) secondary forest (native tree-dominated regrowth up to 15-20 years old), 4) tree plantations (mainly traditional single species exotic or native reforestation), and 5) gallery forest (forest retained along watercourses comprised of remnant trees and forest regrowth). Additionally, we identified two agricultural land use categories: 6) pastures and 7) annual or perennial crops (e.g. pineapple, sugarcane, bananas, heart of palm).

A supervised image classification was implemented using the Rulegen extension in ENVI v. 4.1 and the Quick, Unbiased, Efficient, Statistical Tree algorithm by Loh and Shih (1996). Elevation, topographic moisture index, percent slope derived from a 90 m digital elevation model (DEM), and the Normalized Difference Vegetation Index (NDVI) were used in addition to TM bands 1-5 and 7 to enhance discrimination of forest and landcover types. Training sites for each category were selected from aerial photos, forest inventory maps, and ground reference points collected in the field between 2004 and 2005. The spatial grain of each landcover category was set at a 1 ha minimum mapping unit for comparisons between image dates.

A classification accuracy evaluation for landcover data obtained an average of 94% overall accuracy with a difference of ±3% between dates and an average kappa score 0.93 scaled at -1 to 1 for all image dates (cf. Congalton and Green 1999). Forest categories showed an acceptable degree of accuracy that averaged from 71% for gallery forests to 95% for natural forests. Landscape complexity increased with time generating lower, but acceptable class accuracy above 80% in later image dates for all classes but gallery forests.

We used area summaries for landcover categories from each image date to compare the larger case study area and the Corridor where PSA programs are focused. Differences in rates of change in forest categories were used to compare forest retention and recovery in T1 and T2 within the Corridor. An annual rate of change for each period and forest category was estimated using a standardized rate formula by Puyravaud (2003),

$$r = (1/t_2 - t_1)) \times \ln(A_2/A_1)$$

where A_1 is the forest area at the first time interval (t_1) and A_2 is the forest area at the second time interval (t_2). Additionally, Wilcoxon Signed Rank tests compared the size distribution of patches ≥1 ha in size converted from a forest type to another land use category across T1 and T2. The FRAGSTATS spatial statistics package (v. 3.3 build 5; McGarigal and others 2002) calculated patch cohesion, percentage of like adjacencies, and mean Euclidean nearest neighbor metrics as indicators of connectivity, aggregation, and isolation for the Corridor. We compared fragmentation indices across the three image dates at the landscape level and for each forest type.

Landowner decision making

To help explain landcover changes in T1 and T2 and identify whether forest policies and PSA incentives positively influenced landowner decisions to retain natural forest and participate in reforestation programs, we conducted a livelihoods analysis examining household decisions in the context of national and international economic markets and policies (Geist and Lambin 2001; DFID 2003). A household survey instrument was used to collect data about historical on-farm tree management including natural forest, *charral*, secondary forest, tree plantations, and gallery forest. The survey measured the five livelihood assets (social, human, financial, physical, and natural) and explored the influence of the 1996 Forestry Law and PSA on land use decisions, motivations to enroll land in PSA programs, production options, and future plans for forest currently enlisted in PSA. As PSA is a voluntary program, participants and non-participants were compared across livelihood assets to identify variables likely to influence participation.

We used a FONOFIFO database of all PSA participants (n=510) to randomly select a sample of 99 households within the Corridor. Those receiving reforestation incentives from previous programs (e.g. CAF, CAFA) were included as participants because their payment contracts were continued under the 1996 Forestry Law. A sample of 108 non-participants was selected from the Ministry of Agriculture's 2000 Costa Rican Cattle Census and paired spatially with those in the participant sample. Sample sizes provided a sampling error of ±10% (Salant and Dillman 1994) with only 6 refusals. The unit of analysis was the household, and a research team administered questionnaires via face-to-face survey interviews averaging one hour per household.

Summary data were developed from specific questions regarding on-farm tree management and motivations to participate in PSA programs. A decision tree analysis was used to compare the livelihood assets of incentive program participants and non-participants. Decision-tree thresholds provide the break point values used to identify boundary levels of assets where incentives may induce landowner participation in a PSA program. Participants with forest protection and management contracts were analyzed separately from those with reforestation because ownership of ≥2 ha of forest land is required by the former two PSA options.

Above- and belowground carbon storage in secondary forests

We selected a chronosequence of twelve secondary forest sites developing on former pasture to examine secondary forest development and the potential of these forests to provide environmental services via carbon storage. Secondary forest development as a mode of forest recruitment was probed in landowner surveys, and the selected study sites represent *charral*, secondary forest, and pasture landcover types identified in the land change detection. Sites included: 1) three young sites in the *charral* phase of development, characterized primarily by shrubs and herbaceous cover, 2) nine older secondary forest sites eligible for legal classification as forest by 1996 Forestry Law standards, and 3) four active pastures grazed for at least 18 years. Fifteen sites were located on acidic, highly weathered Ultisols derived from volcanic parent material, and the remaining site was located on an Inceptisol derived from alluvial deposits.

At each site, soil samples were collected from four locations in each of three plots at depths of 0-10, 10-20, and 20-30 cm. Three samples per depth were composited for percent soil carbon determination, and the fourth sample was used for bulk density determination. We derived soil carbon content at the Idaho Stable Isotopes Laboratory, and data are reported on a volume basis.

Within the nine secondary forest sites, three 50×50 m plots were established to determine species and diameter at breast height (1.37 m, dbh) for all trees, palms, and lianas ≥5 cm dbh. When present, dbh measurements were made above buttresses. Data were used to estimate total aboveground biomass using the equation for wet forest stands by Chave and others

(2005) that accounts for differences in wood density among species. Estimates of aboveground biomass were multiplied by 0.5 to determine aboveground carbon storage. Remnant trees comprised of stems ≥60 cm dbh (<1% of all stems at these sites) were removed from the dataset.

For soil carbon analyses, we employed the statistical language R (v. 2.0.1, R Development Core Team 2004). Mean soil carbon storage was analyzed separately by depth class, and linear mixed-effects models (Pinheiro and Bates 2000) were used to examine changes across land use types. Significant differences detected with analysis of variance (ANOVA) were further examined via multiple comparisons procedures.

RESULTS AND DISCUSSION

Patterns of natural forest retention

Notable differences in the status of natural forest occurred between the larger study area and Corridor over a relatively short time period (15 yrs). Land change estimates showed a striking decrease in the annual rate of natural forest loss from -1.43% yr^{-1} in T1 to -0.20% yr^{-1} during T2 inside the Corridor (Table 1). Natural forest loss in T2 occurred primarily outside the Corridor in areas that became an increasingly heterogeneous mixture of pasture, crops, and tree plantations (Fig. 2a; b). This pattern indicates that areas outside the Corridor remained vulnerable to forest loss regardless of the 1996 Forestry Law's forest change restrictions. Reduced forest loss in the Corridor, where a high density of forest protection and management contracts were established during T2, was concurrent with implementation of the 1996 Forestry Law and PSA. High rates of forest loss during T1 were consistent with other forest change studies conducted in the region (Read and others 2001; Sánchez-Azofeifa and others 2003). Significantly larger natural forest patches were converted to other land uses in T1 relative to T2 (p <0.001). Large contiguous forest patches (>150 ha) were removed prior to 1996 (67 in T1 vs. 5 in T2), creating highly fragmented forest conditions in the northeastern portion of the Corridor (Figure 3).

Data from landowner surveys showed that 65% of the total sample population owned natural forest and 59% of these individuals received payments for protection. Forty-four percent of landowners receiving PSA did not intend to clear or harvest any forest. However, 33% of respondents with PSA indicated that they would convert some of their forest to pasture or crops, while 19% would harvest some timber in the absence of PSA and the

Forestry Law's legal restrictions on forest land use change. Therefore, PSA payments provided protection against forest clearing and harvesting. This is in contrast to findings from landowners interviews on Costa Rica's Osa Peninsula where PSA was found to have little to no immediate impact on forest protection (Sierra and Russman 2006).

A landowner's dependence upon his or her farm as a primary source of income constituted the principal livelihood variable differentiating PSA participants from non-participants in the forest protection and management programs ($p < 0.0001$). Participants had a lesser dependence on their farms for income than non-participants, suggesting that individuals whose livelihoods depended less directly on farm income were more likely to participate in PSA. Our observations confirm similar patterns found in this and other regions of Costa Rica (Miranda and others 2003; Zbinden and Lee 2005). However, the PSA program for forest protection effectively competed with other opportunity costs of forest land, in that it was common for landowners with up to 73% of their income derived from the farm to participate in PSA. Production options for private forest remain limited to timber extraction because of the 1996 Forestry Law's ban on forest clearing. Permits to harvest are limited, so those unable to obtain permits have an opportunity cost of foregone production near zero, and thus, can only gain by entering into a PSA contract. Pagiola and others (2002) noted an excess national demand for the PSA protection program, implying that the same amount of forest protection could likely be provided at lower payment rates (Rojas and Aylward 2003).

Forest recruitment: reforestation

Results from landcover comparisons show that forest cover increased over both time periods with positive consequences for environmental services, primarily during T2. A net gain in forest cover of 0.5% yr^{-1} occurred in T1 and 0.6% yr^{-1} in T2 (Table 1), although gains after 1996 were concurrent with greatly reduced natural forest loss. In general, land withdrawn from forest cover may constitute a loss of environmental services such as biodiversity and carbon sequestration (Snider and others 2003). Increased forest cover in the Corridor for both time periods was mainly the result of a large increase in tree plantations (Figure 2a) established in pastures. Tree plantations increased from 19 km^2 in 1986 to 268 km^2, representing 11% of the total land area in 2001 (Figure 3). These figures compared favorably to the cumulative total of ~380 km^2 reported to have been planted regionally up to 2001 (COSEFORMA 1995; Méndez 2003).

The rate of tree plantation establishment decreased from 24 to 4.6% yr^{-1} during T1 and T2, respectively (Table 1), with significantly smaller pastures planted after 1996 ($p < 0.05$). A number of tree plantations were either harvested or overtaken by natural regeneration by 2001 (data not shown). Although we detected substantial increases in forest cover under plantations, regional figures show that on an area basis, PSA for forest protection (51%) and management (33%) were favored over reforestation programs (17%) (Méndez 2003). These statistics reflect national priorities to reduce forest loss via PSA for forest protection (Snider and others 2003) rather than promote forest recruitment through reforestation. Because forest plantation conversion to other land uses is permitted, their long-term contribution to forest cover and environmental services in this landscape is uncertain.

The trends described above indicate that reforestation incentives fueled a rapid expansion of tree plantations in the Corridor since 1986. Nearly one third of all landowners interviewed (31%) maintained tree plantations on their farms, and the majority (60%) were established through PSA reforestation contracts. Primary motivations for plantation establishment included perceived value of the wood (40%), meeting conservation objectives such as biodiversity protection (20%), and availability of payments (17%). Most reforested land was converted from pasture (88%) while 12% was formerly crop land. Fifty-three percent of landowners indicated satisfaction with the level of PSA payments, with remaining landowners indicating that payments did not meet expected costs. Of those with PSA, a majority (68%) would not have reforested without payments to cover establishment and maintenance costs, demonstrating the importance of financial incentives to induce landowner participation in reforestation activities.

Of those with reforestation under the PSA program, a majority (59%) intended to plant another crop of trees after harvesting their current plantation while a quarter (24%) indicated they would not replant, and 17% remained undecided until final harvests. Landowners reforesting without PSA incentives showed similar patterns. The majority of landowners have adopted forest plantations as a viable economic activity, competitive with other land use options and economic opportunities.

Reforestation incentives were a critical factor in forest cover gained from tree plantations during T1 and T2. A landowner's dependence on his or her farm as a primary source of income was the primary livelihood variable differentiating PSA reforestation participants from non-participants ($p < 0.0001$). However, a division between groups occurred at the point where 16% of the household income was derived from the farm, with individuals more likely to participate below this point. Results show that PSA for reforestation remains uncommon for landowners moderately dependent upon their farms as a source of income, indicating that payment rates are not adequate to motivate most farm-dependent individuals to forgo current production systems.

Forest recruitment: secondary vegetation and gallery forest

Successional vegetation occupied between 8 and 10% of the Corridor area at any one point in time, maintaining persistent areas of natural regeneration in the Corridor (Figure 3). However, the total land area in the early successional *charral* phase declined during the study period from 9% in 1986 to 4% in 2001 (Figure 2a), indicating that the outlook for recruiting new secondary forest stands was lower after 1996. Although land area in secondary forest increased slightly after 1996, the patch size of both secondary forest and *charral* areas recruited significantly declined ($p < 0.001$). Additions to the area occupied by secondary forest (Table 1) during T2 accounted for some of the losses in the *charral* phase as succession proceeded.

Our landcover data show that forest recruitment via secondary succession may represent only temporary gains in connectivity and short-lived opportunities for habitat restoration. An overall decline in land area occupied by *charral* (Table 1) indicates that landowners abandoned very little pasture land throughout the study period, as observed previously by Read and others (2001). The low level of secondary forest establishment in the Corridor did not follow patterns of agricultural abandonment conducive to forest recruitment encountered elsewhere in Costa Rica (Arroyo-Mora and others 2005). The amount of pasture land allowed to recover to the *charral* stage was offset by a greater amount being returned to pasture in both T1 and T2. This observation is corroborated by data from landowner surveys indicating that only 13% of respondents had *charral* on their property. Of these individuals, 56% maintained *charral* for economic reasons, while 20% cited conservation reasons. The role of economics in decisions to maintain *charral* shows that natural forest regeneration in the Corridor was likely limited by PSA incentives for reforestation, agricultural export opportunities, and restrictions in the 1996 Forestry Law prohibiting land use change.

Survey data supports the observation that much of the land converted to *charral* (68%) or secondary forest during our study period previously existed as pasture (Figure 2; 4). Although *charral* and secondary forest occupy a small amount of land area relative to natural forest, these forest types are ecologically important as sites for forest recruitment, carbon sequestration, and habitat restoration (Holl and Kapelle 1999). *Charral* typically persists on abandoned land for a short period of time before a tree canopy develops, but restrictions on forest clearing provide incentives for landowners to inhibit the development of secondary forest (Sierra and Russman 2006). Surveyed landowners planned to clear 43% of existing *charral* for pasture or agricultural use in the future, thus limiting the potential for carbon storage (Murty and others 2002).

Transitions from pasture to secondary forest reveal differences in carbon storage at shallow soil depths. Pastures contained a greater amount of mineral soil carbon at 0-10 cm relative to *charral* and secondary forest, but there was high variability within land use classes (Table 3). Mineral soil carbon storage in pastures rapidly decreased with depth, and both *charral* and secondary forests had significantly higher soil carbon storage than did pastures at depths of 10-30 cm (Table 3). High levels of soil carbon storage in *charral* at 10-30 cm depth likely occurs from shifts in rooting depth and subsequent alteration of organic carbon inputs to the soil at an early successional phase (Jackson and others 1996; Jobbágy and Jackson 2000). A decline in soil carbon storage at these depths in secondary forest relative to *charral* was not unexpected, as these sites were dominated by more deeply rooted trees.

Managed crops remain a competitive land use with secondary forest on former pasture (Figure 4), and agricultural transitions can decrease soil carbon stores up to 30% during the first decades of cultivation (Murty and others 2002). Survey respondents also suggested reforestation as another common land use option on former pasture land (Figure 4), and although plantations often increase soil carbon storage in the tropics (Silver and others 2000), this is not always the case (Powers 2004). In relation to competing land uses, secondary forests may provide considerable carbon services.

Above- and belowground carbon storage rapidly increased toward values observed in primary forest following secondary forest establishment. For 0-30 cm, soil carbon storage in secondary forests was slightly lower (70.9 Mg C ha^{-1}) than the regional mean of 82.2 Mg C ha^{-1} in primary forests (Powers and Schlesinger 2002). Aboveground, secondary forest stands appear to pass through a period of low biomass accumulation and reach the point of stem exclusion after 20 to 25 years of development (Figure 5). Following this phase, 25 to 30 year old secondary forests had aboveground carbon stocks equivalent to those in primary forests of the region (Figure 5; Clark and Clark 2000). The carbon services provided by secondary forest rival those of natural forest and merit greater attention from forest management and policy perspectives. Our data show that forest policies and incentives have effectively influenced land-use decisions for tree plantations, and similar incentives for natural regeneration could enhance carbon storage as a targeted PSA environmental service.

In addition to carbon storage, benefits accruing from secondary forest recovery include forest structural connectivity, natural habitat development, and new timber resources (Finegan 1992; Lamb and others 1997). Secondary forests provide a number of potential economic and restoration opportunities that contribute positively to the goals of the San Juan-La Selva Biological Corridor. The existence of competing land uses with greater financial returns than secondary forest suggests that financial incentives and technical support may be necessary to secure the environmental services provided by these forests. The recent introduction of PSA for natural regeneration (FONAFIFO 2006) represents significant progress in acknowledging the benefits of secondary forest, though the program remains confined to western Costa Rica.

Gallery forests also have important consequences for recruiting forest cover in the Corridor, increasing from 2 to 6% of the total land area during T1 and T2, respectively (Table 1). Linear forest arrangements of remnant trees and secondary vegetation were retained along waterways as surrounding forests were cleared in T1. We interpreted an increase in post-1996 gallery forests as forest recruitment because few large patches of natural forest were removed in T2. Forest land along perennial rivers and streams has received protection by laws designed to conserve water resources since 1942. Eighty-five percent of landowners sampled in the Corridor had land occupied by gallery forest. Recruitment patterns in T2 reflect a social commitment to protecting water resources as 87% of survey respondents gave conservation-oriented reasons for retaining tree cover in riparian areas.

Forest and landscape connectivity

We analyzed the spatial and temporal arrangement of forests in the Corridor as an indicator of physical connectivity among protected and privately owned forests. Connectivity varied across T1 and T2 for total forest cover (landscape indices) and individual forest types (class indices). Landscape indices in the Corridor showed a decline in connectivity and aggregation among all forest patches during T1, and a maintenance of conditions with some enhanced connectivity during T2 (Table 2). These patterns reflected the higher rate of natural forest loss observed in T1 relative to T2 (Table 2), but can be partially explained by the development of increasingly heterogeneous forest conditions. At the class level, natural forests comprised the majority of total forest cover and became increasingly distant from one another over time, reflected by increased isolation and decreased aggregation (Table 2). In contrast, patterns in reforestation, forest regrowth, and gallery forest showed trends with an overall positive impact on forest connectivity and aggregation (Table 2). Patches of reforestation and secondary forest regrowth tended to aggregate in a few areas of the Corridor (Figure 3).

Greater natural forest retention in T2 and recruitment throughout the study period indicates that the 1996 Forest Law and prior reforestation programs contributed to a net increase in forest connectivity. Landowner decisions to participate in PSA programs have increasingly affected the process of reconnecting forests in this landscape. Though monocultures of fast growing exotic species occupy many of the reforested areas, a recent shift toward native tree species has occurred. Native species plantations have the potential to support diverse understory flora (Cusack and Montagnini 2004) and attract wildlife (Lamb and others 1997), but the overriding homogeneity of tree plantations may detract from natural forest connectivity. During T1 some tree plantations with low species and structural diversity replaced natural forests following short-term use as pasture. After this land use change became illegal in T2, significantly fewer natural forest patches were converted to tree plantations ($\Delta T1 > \Delta T2$, $p < 0.001$).

Secondary forests play a role in maintaining forest structural connectivity, often developing on land adjacent to natural forest (Figure 3). The benefits of secondary forest cover on the landscape in terms of forest connectivity, biodiversity value, and carbon services may outweigh those of tree plantations in light of 1996 Forestry Law objectives. As secondary vegetation reaches a successional stage with at least 60 tree stems >15 cm dbh ha^{-1}, it is legally classified as forest and can no longer be cleared for alternate land uses. Because plantations are harvested on short rotations and can be legally converted to non-forest uses, retention of new forest cover through secondary succession is more likely to be a permanent type of forest cover. However, secondary forests are likely to have a less positive economic impact on local livelihoods when compared to plantations.

Many of Costa Rica's recognized corridor areas resemble stepping stones of forest habitat within agriculturally-dominated landscapes because intensively managed crops typically support little or no tree cover. The implications of the 1996 Forestry Law in conjunction with the data reported here reflect on an emerging importance of forest recruitment via a variety of pathways. As natural forests were replaced by reforestation and secondary forests, a fundamental change in forest structural connectivity occurred. This highlights the need to examine the functional role of these new forest connections where forest cover is best characterized as a mosaic of habitats with variable economic and ecological potential.

CONCLUSIONS

Costa Rica's innovative strategies to maintain private forest land and environmental services showed notable progress toward these goals in the Corridor. The rate of natural forest loss was substantially less after 1996 relative to the previous time period. Legal restrictions in the 1996 Forest Law forbidding land use change reduced the opportunity cost of forest land, influencing landowners moderately dependent on their farms for income to participate in the PSA forest protection program. Continued high rates of natural forest loss outside the Corridor after 1996 indicated that restrictions on forest clearing without the benefit of PSA were not sufficient to induce forest retention in this region.

PSA directly influenced landowner decisions to substantially increase forest recruitment during the study period. Specifically, reforestation incentives prior to PSA led to a dramatic increase in plantation forests during T1, while a slower increase occurred following PSA implementation in T2. Forest recruitment via secondary forest development occupied a relatively constant amount of land area in the Corridor through time. However, disincentives for secondary forest development existed in the form of lost land use opportunities once an area returned to forest. Carbon services provided by 25-30 year old secondary forests were similar to those in primary forest, suggesting that these forests deserve greater attention from a land management perspective.

Positive outcomes of the 1996 Forestry Law were further illustrated by changes in forest cover dynamics that enhanced forest structural connectivity in the Corridor in T2, relative to T1. In the future, adaptations of the PSA program such as that recently implemented for natural regeneration in western Costa Rica will continue to provide flexibility in tailoring the program to diverse and changing landscapes. As a case study, the Costa Rican experience with PSA provides evidence that environmental service payment programs in conjunction with legal forest protection are effective in retaining natural forest and recruiting new forest cover when focused in the Corridor as a priority conservation area. PSA has been tailored to fit Costa Rica's socioeconomic conditions, but shows promise as an effective conservation approach with prospects for adaptation to other settings.

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Tables

Table 1. The amount of forest lost or gained during each time period estimated by subtracting the total area for each forest category in the corridor from the previous year's land cover data (Δ*T1*=1986-96, Δ*T2*=1996-01). The annual rates of forest cover change by type and net forest gain before and after 1996 were estimated using the formula by Puyravaud (2003) and expressed as percentages. Net forest cover includes all five forest types.

Forest cover type	**Δ*T1* (km^2)**	**Δ*T1* yr^{-1} (%)**	**Δ*T2* (km^2)**	**Δ*T2* yr^{-1} (%)**
Natural forest	-179	-1.43	-12	-0.20
Reforestation	194	24.15	55	4.57
Charral	-42	-2.25	-60	-8.93
Secondary forest	69	18.95	20	4.31
Gallery forest	36	5.21	48	8.66
Net forest cover	78	0.47	50	0.58

Table 2. Fragmentation indices for the Corridor landscape and individual forest classes indicating changes in physical connectivity at each landcover date. The level of isolation was determined using Euclidean nearest neighbor distance (ENN) to measure isolation, patch cohesion (PC) as an indicator for physical connectivity among like patches, and percentage of like adjacencies (PLA) as a measure of aggregation of similar patches.

	Isolation ENN (m)			**Connectivity PC (%)**			**Aggregation PLA (%)**		
Category	**1986**	**1996**	**2001**	**1986**	**1996**	**2001**	**1986**	**1996**	**2001**
Landscape	256.2	241.8	249.0	99.3	99.0	98.9	89.8	88.1	88.3
Natural forest	130.6	135.4	142.7	99.76	99.68	99.68	94.83	94.02	93.91
Reforestation	337.0	202.3	187.9	86.59	97.06	97.91	71.34	81.81	81.36
Charral	164.3	191.1	250.9	93.28	93.33	93.82	74.14	75.20	77.28
Secondary forest	526.4	215.7	227.9	83.46	89.09	92.68	67.39	70.48	74.05
Gallery forest	238.5	216.9	188.1	87.57	89.20	92.19	67.66	71.78	74.57

Table 3. Means of mineral soil carbon storage ± one standard error across all land use types and soil depths. Reported *p*-values were derived from individual ANOVAs performed for each soil depth. Superscripted letters represent the result of means separation performed using pre-planned contrasts in the Multcomp package of R. Different superscripted letters represent significant differences among categories.

Soil depth	**Pasture soil carbon (Mg ha^{-1})**	***Charral* soil carbon (Mg ha^{-1})**	**Secondary forest soil carbon (Mg ha^{-1})**	***p*-value**
0-10 cm	43.69 ± 3.09^{a}	34.65 ± 2.31^{b}	35.70 ± 1.13^{b}	0.012
10-20 cm	18.71 ± 1.38^{a}	25.00 ± 1.63^{b}	20.65 ± 0.69^{c}	0.0048
20-30 cm	12.60 ± 0.65^{a}	17.53 ± 1.63^{b}	14.57 ± 0.73^{c}	0.0167

Figures

Figure 1. Map of the San Juan – La Selva Biological Corridor, connecting national parks and protected areas, and the larger study area. Depicted natural forest cover is for year 2000 (Atlas of Costa Rica 2004).

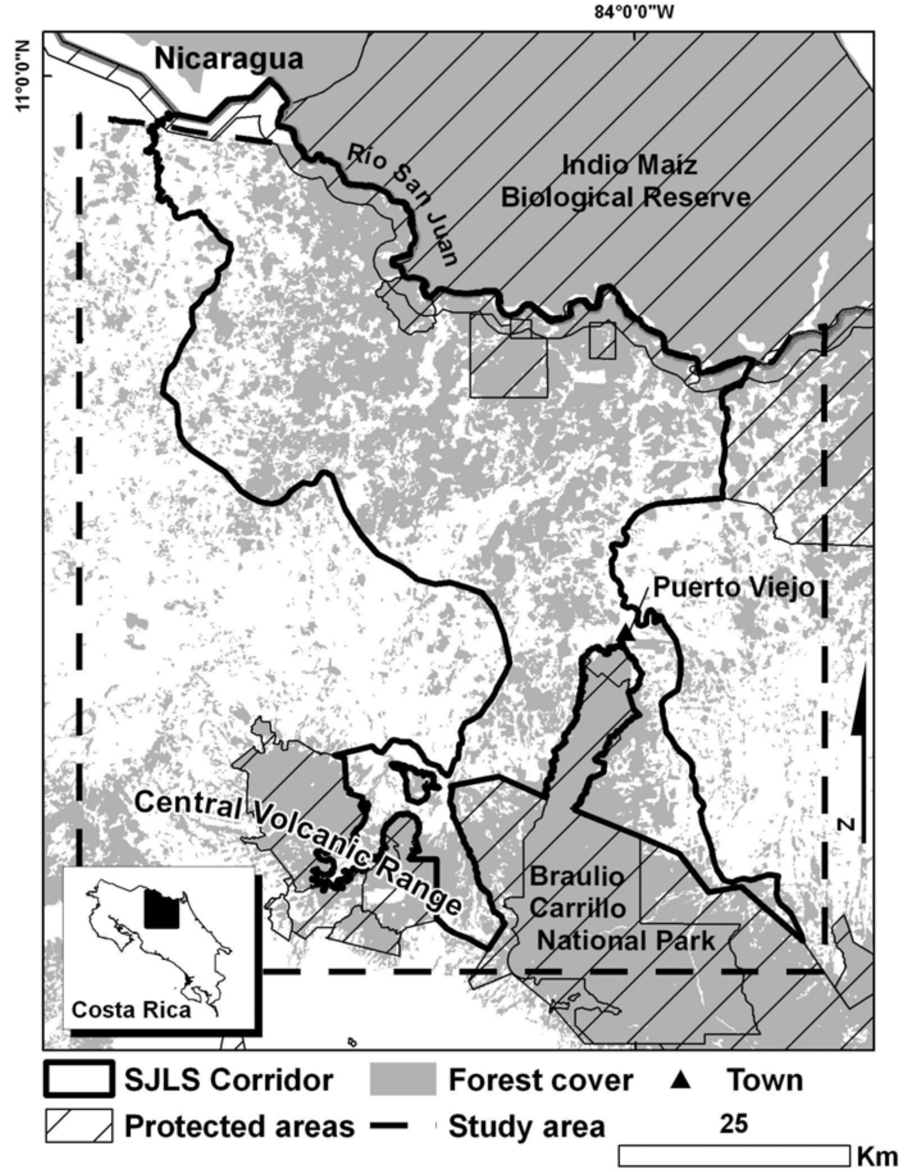


Figure 2. Area differences for each time interval for (a) the five forest categories and (b) two agricultural categories observed at the extent of the study area (6,349 km^2) and the San Juan – La Selva Biological Corridor (2,425 km^2). Dotted lines above the natural forest category show the top of the bar in year 2001, indicating that a greater percentage of natural forest loss occurred outside of the Corridor after 1996.

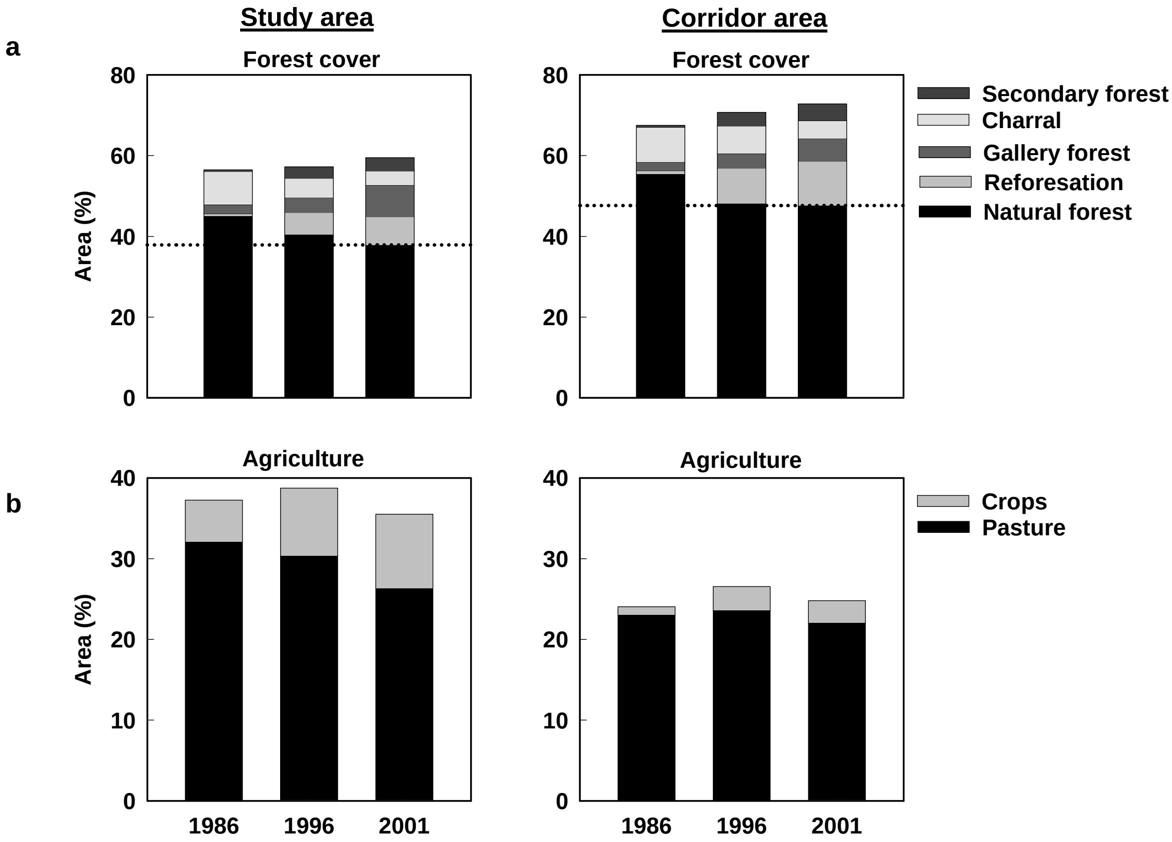


Figure 3. Mapped forest cover in the San Juan – La Selva Biological Corridor depicting major landscape changes at each time interval using the forest categories natural forest (dark green), forest regrowth (*charral* and secondary forest, bright green), and reforestation (orange).

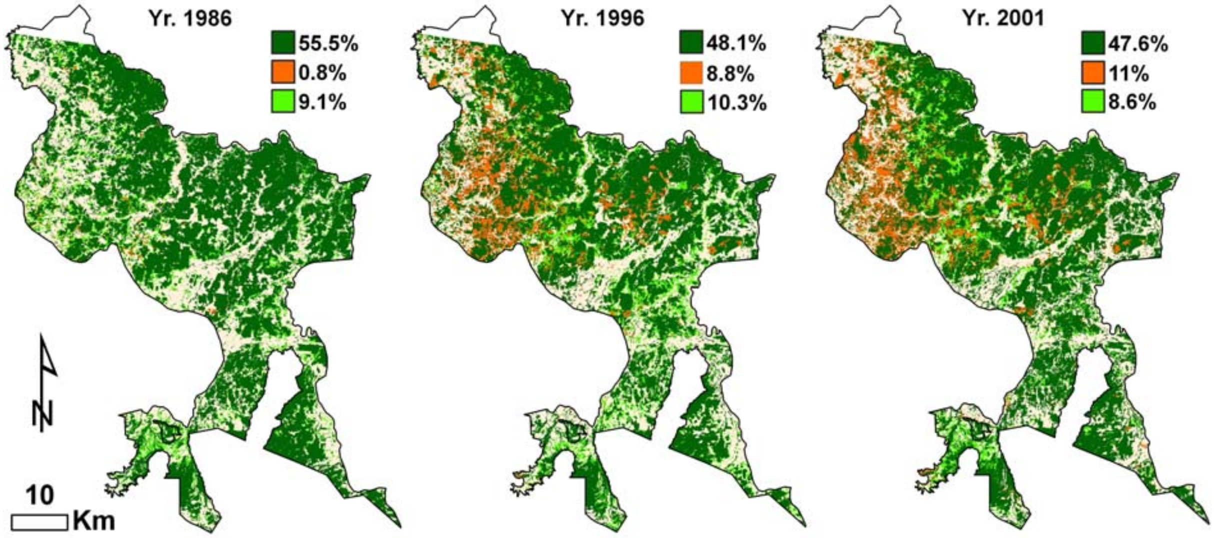


Figure 4. Amount of pasture converted to another forest or landcover type in the San Juan – La Selva Biological Corridor during time periods T1 and T2.

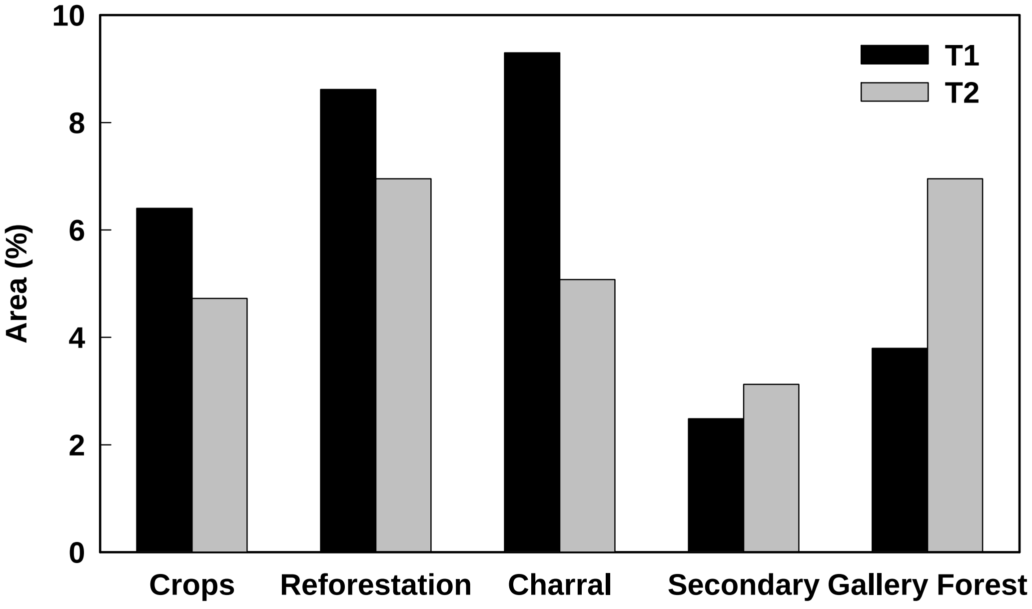
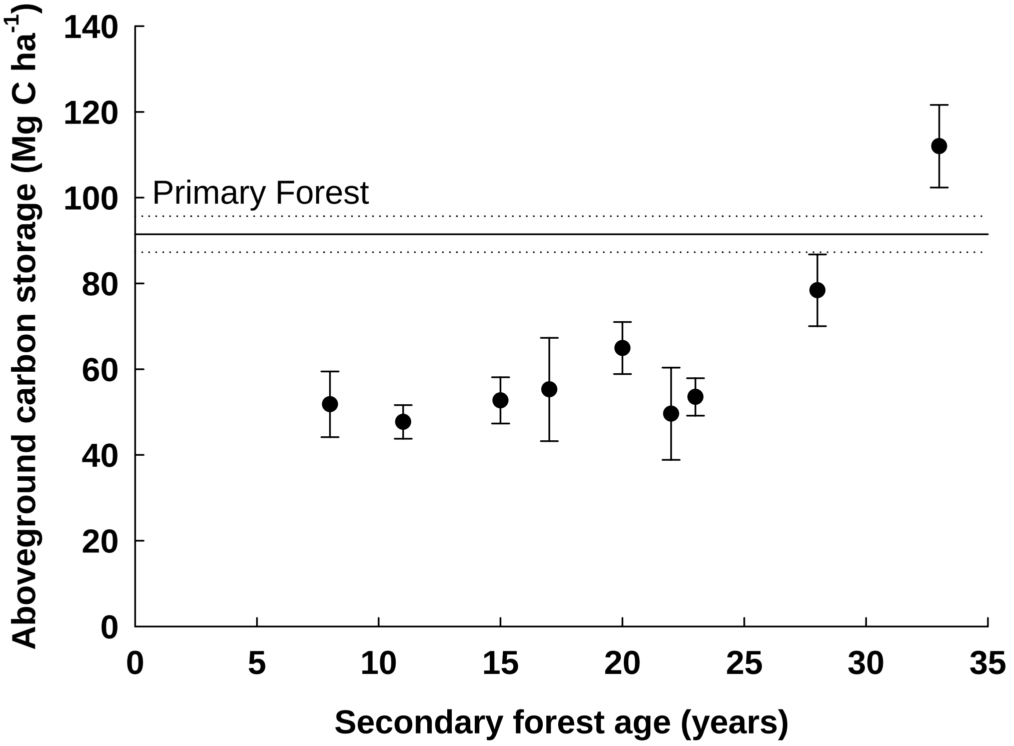


Figure 5. Mean aboveground carbon storage ± one standard error for each secondary forest site. The solid and dotted horizontal lines represent mean aboveground carbon storage and one standard error, respectively, as measured in undisturbed primary forests at the La Selva Biological Station (Clark and Clark 2000). Values were calculated as one half of aboveground biomass estimates for all stems ≥10 cm dbh in plots ≥4 ha.



Appendices

Appendix 1. Results from Indicator Species Analysis ([1]Dufrene and Legendre 1997) using 144 forest plots and forest types derived from cluster analysis. Forest type abbreviations and number of plots for each type are listed in Table 1 of Chapter 1. Significance tests are from 1000 randomizations used with Monte Carlo tests.

		Forest	**(IV)**	**IV - randomized groups**		
Family	**Tree species**	**type**	**Indicator Value**	**Mean**	**S.Dev**	***p ****
Fabaceae/Mim.	*Pentaclethra macroloba*	Pc	52.1	15.2	4.53	0.002
Meliaceae	*Guarea gentryi*	Pc	13.5	9.6	9.28	0.228
Rubiaceae	*Simira maxonii*	Pc	11.1	7.7	8.07	0.12
Sapotaceae	*Pouteria sp.*	Pc	8.3	9.9	9.07	0.39
Moraceae	*Brosimum lactescens*	Pc	7.7	12.2	6.49	0.822
Flacourtiaceae	*Laetia procera*	Pc	4.4	11	9.18	0.818
Fabaceae/Pap.	*Lecointea amazonica*	Pc	4.4	7.6	8.3	0.61
Lecythidaceae	*Eschweilera longirachis*	Pc	4.3	7.6	8.02	0.67
Sapotaceae	*Pouteria belizensis*	Pc	4.2	7.1	7.08	0.626
Sapotaceae	*Pouteria campechiana*	Pc	3.5	8.9	9.86	0.806
Fabaceae/Pap.	*Lonchocarpus ferrugineus*	Pc	3.1	7.1	7.17	0.908
Arecaceae	*Socratea exorrhiza*	Pp	21.6	15.3	3.34	0.048
Sapotaceae	*Pouteria durlandii*	Pp	11.4	12.1	7.21	0.426
Simaroubaceae	*Simarouba amara*	Pp	6.5	12.1	9.2	0.76
Annonaceae	*Xylopia sericophylla*	Pp	6.3	9.6	9.42	0.408
Sapotaceae	*Pouteria calistophylla*	Pp	5.7	8.4	9.01	0.466
Arecaceae	*Bactris sp.*	Pp	5.1	10.4	7.9	0.726
Apocynaceae	*Tabernaemontana alba*	Pp	3.8	8.3	9.4	0.852
Humiriaceae	*Humiriastrum diguense*	Pp	3.8	7	6.71	0.842
Elaeocarpaceae	*Sloanea meianthera*	Pp	3.8	7.6	8.25	0.83
Sapotaceae	*Pouteria cuspidata*	Pp	3.8	7.7	8.11	0.798
Fabaceae/Mim.	*Abarema macradenia*	Pp	3.8	8.2	10.37	0.76
Fabaceae/Mim.	*Inga sp.07*	Pp	3.8	8.2	9.68	0.756
Polygonaceae	*Coccoloba tuerckheimii*	Pp	2.9	7.9	8.17	0.854
Vochysiaceae	*Qualea paraensis*	Qp	43.5	12.7	7.46	0.014
Arecaceae	*Welfia georgii*	Qp	34.7	15.4	3.96	0.002

Arecaceae	*Prestoea decurrens*	Qp	34.4	11.4	9.39	0.032
Apocynaceae	*Couma macrocarpa*	Qp	28.8	12.2	7.97	0.04
Fabaceae/Pap.	*Dipteryx panamensis*	Qp	27.5	12.6	7.46	0.05
Vochysiaceae	*Vochysia ferruginea*	Qp	25.9	12.9	7.17	0.068
Fabaceae/Mim.	*Enterolobium schomburgkii*	Qp	21.6	11.4	9.24	0.118
Chrysobalanaceae	*Licania sparsipilis*	Qp	12.5	9	9.98	0.172
Lepidobotryaceae	*Ruptiliocarpon caracolito*	Qp	12.5	8.1	8.22	0.144
Burseraceae	*Tetragastris panamensis*	Qp	12.1	12.9	7.13	0.434
Myristicaceae	*Otoba novogranatensis*	Qp	8.6	8.7	8.97	0.296
Chrysobalanaceae	*Licania costaricensis*	Qp	8.3	7.6	7.62	0.254
Myrtaceae	*Eugenia sp.*	Qp	8.3	7.4	8.33	0.238
Chrysobalanaceae	*Licania kallunkiae*	Qp	8.3	7.3	7.26	0.216
Sapindaceae	*Cupania livida*	Qp	8.3	7.5	8.1	0.204
Lecythidaceae	*Eschweilera integrifolia*	Qp	8.3	7.2	6.84	0.196
Sapotaceae	*Manilkara aff. staminodella*	Qp	8.3	7.6	8.07	0.192
Chrysobalanaceae	*Parinari excelsa*	Qp	8.3	7.4	8.14	0.19
Rubiaceae	*Ferdinandusa panamensis*	Qp	8.3	7.1	7.7	0.178
Sapotaceae	*Micropholis melinoniana*	Qp	7.7	8	8.93	0.282
Arecaceae	*Astrocaryum confertum*	Qp	6.8	8.7	8.95	0.314
Fabaceae/Pap.	*Dussia sp.02*	Qp	6.2	9.7	11.17	0.416
Euphorbiaceae	*Pera arborea*	Qp	4.9	9.3	10.25	0.546
Sapotaceae	*Pouteria reticulata*	Qp	4.2	9.3	9.01	0.67
Sapotaceae	*Pouteria silvestris*	Qp	2.1	7.5	8.31	1
Rutaceae	*Zanthoxylum panamense*	Qp	1.8	7.5	8.39	1
Magnoliaceae	*Talauma gloriensis*	Qp	1.6	8.9	9.84	0.996
Arecaceae	*Euterpe precatoria*	Pd	34.1	15.4	5.14	0.006
Sapotaceae	*Elaeoluma glabrescens*	Pd	32.6	12.6	7.35	0.036
Humiriaceae	*Vantanea barbourii*	Pd	25.3	12	8.43	0.064
Chrysobalanaceae	*Licania affinis*	Pd	24.8	13	7.83	0.076
Fabaceae/Pap.	*Vatairea lundellii*	Pd	22.4	10.3	8.15	0.098
Lecythidaceae	*Eschweilera sp.02*	Pd	20	7.8	8.15	0.076
Moraceae	*Brosimum guianense*	Pd	15.8	12.2	8.3	0.21
Fabaceae/Mim.	*Balizia elegans*	Pd	11.2	10.8	9.28	0.358
Lecythidaceae	*Lecythis ampla*	Pd	10.8	10.3	9.12	0.314

Sapotaceae	*Micropholis crotonoides*	Pd	9	11.9	7.86	0.548
Fabaceae/Caes	*Macrolobium hartshornii*	Pd	8.9	7	6.68	0.146
Quiinaceae	*Lacunaria panamensis*	Pd	8.3	7.5	8.25	0.22
Clusiaceae	*Calophyllum brasiliense*	Pd	5.3	11.7	9.96	0.736
Podocarpaceae	*Podocarpus guatemalensis*	Pd	5.2	8.4	8.83	0.55
Chrysobalanaceae	*Couepia polyandra*	Pd	5.1	10.3	8.87	0.734
Ulmaceae	*Ampelocera macrocarpa*	Pd	3.7	8.9	9.21	0.77
Lecythidaceae	*Eschweilera calyculata*	Pd	3.6	9.4	9.5	0.77
Lauraceae	*Ocotea insularis*	Ma	43.3	9	9.18	0.006
Arecaceae	*Iriartea deltoidea*	Ma	26.6	15.8	4.27	0.038
Cecropiaceae	*Cecropia insignis*	Ma	22.5	9.4	8.85	0.116
Flacourtiaceae	*Casearia sp.*	Ma	22.2	8.3	9.19	0.084
Clusiaceae	*Dystovomita paniculata*	Ma	22.2	8.4	9.52	0.084
Fabaceae/Mim.	*Inga sp.05*	Ma	18.8	9.9	9.9	0.15
Sapotaceae	*Chrysophyllum colombianum*	Ma	17.8	11.4	8.3	0.18
Meliaceae	*Guarea kunthiana*	Ma	17.8	11.7	8.29	0.164
Chrysobalanaceae	*Maranthes panamensis*	Ma	17.8	12	8.52	0.134
Fabaceae/Pap.	*Andira inermis*	Ma	17.5	8.8	9.82	0.124
Melastomataceae	*Mouriri gleasoniana*	Ma	16.6	8.8	9.59	0.13
Dichapetalaceae	*Tapura guianensis*	Ma	15.4	11.5	9.37	0.194
Chrysobalanaceae	*Hirtella triandra*	Ma	14.9	12.8	10.59	0.274
Hippocastanaceae	*Billia colombiana*	Ma	14.9	10.1	8.8	0.222
Meliaceae	*Cedrela odorata*	Ma	13.6	8.6	9.1	0.156
Cecropiaceae	*Pourouma minor*	Ma	10.2	11.2	7.92	0.412
Lauraceae	*Ocotea sp. 01*	Ma	10.1	6.9	7.23	0.098
Moraceae	*Brosimum panamense*	Ma	9.4	7.5	7.81	0.144
Dichapetalaceae	*Stephanopodium costaricense*	Ma	7.6	8.2	8.78	0.242
Elaeocarpaceae	*Sloanea sp.*	Ma	7.5	10	8.29	0.472
Cecropiaceae	*Cecropia obtusifolia*	Ma	7	8.1	8.98	0.29
Burseraceae	*Protium sp.*	Ma	6.7	7.9	7.98	0.334
Annonaceae	*Rollinia pittieri*	Ma	6.5	8.2	8.75	0.314
Myristicaceae	*Virola sp.*	Ma	6.4	7.3	7.59	0.39
Celastraceae	*Quetzalia occidentalis*	Ma	5.7	7.2	7.29	0.456
Fabaceae/Pap.	*Lonchocarpus sp. 01*	Ma	5.5	8.1	9.52	0.46

Aquifoliaceae	*Ilex skutchii*	Ma	4.9	9.2	8.98	0.536
Rubiaceae	*Guettarda sp.*	Ma	4.2	8.6	9.14	0.732
Combretaceae	*Terminalia bucidoides*	Ma	4.1	10.1	10.08	0.696
Meliaceae	*Guarea sp. 01*	Cy	100	9	9.99	0.002
Sapotaceae	*Pouteria sp.03*	Cy	100	8.9	9.87	0.002
Cyatheaceae	*Cyathea microdonta*	Cy	92.1	10	9.99	0.002
Melastomataceae	*Conostegia rufescens*	Cy	79.8	10.5	9.83	0.002
Fabaceae/Mim.	*Inga sp.02*	Cy	66.7	7.6	8.34	0.002
Fabaceae/Mim.	*Inga sertulifera*	Cy	54.9	8.7	8.61	0.002
Sapotaceae	*Pouteria sp.04*	Cy	53.3	8.1	8.82	0.004
Lauraceae	*Nectandra sp. 01*	Cy	50.8	10.2	11.37	0.008
Moraceae	*Ficus sp.*	Cy	42.6	10.2	10.2	0.01
Meliaceae	*Guarea glabra*	Cy	32.8	7	8.06	0.034
Fabaceae/Pap.	*Pterocarpus rohrii*	Cy	31.2	12.4	9.56	0.038
Cunoniaceae	*Weinmannia sp.*	Cy	26.7	8.8	10.47	0.1
Icacinaceae	*Calatola costaricensis*	Cy	24.8	8	8.65	0.074
Meliaceae	*Guarea bullata*	Cy	23.4	12.1	8.62	0.102
Clusiaceae	*Tovomita weddelliana*	Cy	23	9.1	10.24	0.104
Myrsinaceae	*Ardisia fimbrillifera*	Cy	19.7	9	10.82	0.126
Sapotaceae	*Pouteria sp.05*	Cy	18	10.2	10.04	0.178
Moraceae	*Naucleopsis naga*	Cy	17.9	11.1	9.52	0.168
Myrtaceae	*Eugenia sp. 01*	Cy	16.3	9.2	9.5	0.162
Malvaceae	*Hampea appendiculata*	Cy	15.6	9.8	9.64	0.19
Fabaceae/Mim.	*Inga chocoensis*	Cy	14.6	9.5	9.23	0.218
Fabaceae/Pap.	*Dussia sp. 01*	Cy	13.1	9.5	9	0.22
Fabaceae/Mim.	*Inga alba*	Cy	8.4	11.4	7.42	0.552
Anacardiaceae	*Tapirira guianensis*	Ta	36.5	13.8	7.01	0.014
Icacinaceae	*Dendrobangia boliviana*	Ta	29.5	12.2	8.31	0.042
Humiriaceae	*Sacoglottis trichogyna*	Ta	29.3	11.4	7.79	0.036
Bignoniaceae	*Jacaranda copaia*	Ta	25	8.4	8.75	0.08
Olacaceae	*Minquartia guianensis*	Ta	24.5	12.4	8.35	0.074
Ochnaceae	*Cespedesia macrophylla*	Ta	20.8	12.5	7.86	0.1
Sapotaceae	*Manilkara zapota*	Ta	17.6	11.1	7.34	0.15
Burseraceae	*Protium pittieri*	Ta	16.2	11.4	7.53	0.198
Bombacaceae	*Quararibea bracteolosa*	Ta	15.2	10.1	9.4	0.174
Lecythidaceae	*Eschweilera sp.03*	Ta	14	8.5	8.79	0.142
Annonaceae	*Unonopsis sp.*	Ta	13.7	9.2	9.51	0.194

Chrysobalanaceae	*Licania hypoleuca*	Ta	11.6	12.6	7.77	0.414
Boraginaceae	*Cordia megalantha*	Ta	10.1	8.9	9.69	0.176
Sapotaceae	*Manilkara chicle*	Ta	9.8	10.9	8.76	0.408
Burseraceae	*Protium ravenii*	Ta	9.1	9.5	9.41	0.33
Sapindaceae	*Cupania sp.*	Ta	8.3	11.4	10.28	0.498
Sapotaceae	*Pouteria filipes*	Ta	7.6	11.8	7.97	0.656
Sapotaceae	*Pouteria sp.06*	Ta	7.2	7.6	8.52	0.302
Melastomataceae	*Miconia multispicata*	Ta	6.6	7.3	7.85	0.342
Euphorbiaceae	*Hyeronima alchorneoides*	Ta	6	9.9	8.93	0.522
Sterculiaceae	*Sterculia recordiana*	Ta	5.9	11.7	9.39	0.688
Annonaceae	*Guatteria aeruginosa*	Ta	5.7	11.3	10.95	0.59
Apocynaceae	*Aspidosperma spruceanum*	Ta	4.7	9.1	9.02	0.578
Fabaceae/Pap.	*Ormosia intermedia*	Ta	4.5	11.1	9.67	0.792
Fabaceae/Caes	*Macrolobium costaricense*	Ta	3.1	10.8	8.68	0.94
Fabaceae/Mim.	*Stryphnodendron microstachyum*	Va	32.4	11.9	8.01	0.03
Vochysiaceae	*Vochysia allenii*	Va	29.3	13.7	7.91	0.068
Malpighiaceae	*Byrsonima crispa*	Va	29.2	10.9	8.91	0.05
Burseraceae	*Protium schippii*	Va	23.1	8.7	10.06	0.1
Bombacaceae	*Pachira aquatica*	Va	18.6	10.2	9.09	0.142
Flacourtiaceae	*Casearia arborea*	Va	17.8	10.4	8.5	0.156
Fabaceae/Mim.	*Inga oerstediana*	Va	15.4	7.9	8.54	0.094
Euphorbiaceae	*Conceveiba pleiostemona*	Va	14.2	10.8	8.81	0.256
Fabaceae/Mim.	*Zygia sp.*	Va	12.9	8.3	9.52	0.142
Meliaceae	*Carapa guianensis*	Va	12.3	13.7	7.77	0.46
Myrsinaceae	*Parathesis trychogyne*	Va	11.2	8.4	8.45	0.204
Flacourtiaceae	*Macrohasseltia macroterantha*	Va	10.4	10	8.8	0.336
Meliaceae	*Guarea grandifolia*	Va	10.4	9.1	9.52	0.242
Euphorbiaceae	*Alchorneopsis floribunda*	Va	9.6	10.4	8.61	0.406
Fabaceae/Pap.	*Dussia macroprophyllata*	Va	9.2	12.1	8.16	0.554
Meliaceae	*Guarea sp.03*	Va	7.5	8.8	9.38	0.262
Clethraceae	*Clethra mexicana*	Va	7.2	11.1	8.64	0.566
Euphorbiaceae	*Hyeronima oblonga*	Va	7.2	10	9.06	0.46
Fabaceae/Pap.	*Hymenolobium*	Va	6.7	7.5	8.12	0.344

	mesoamericanum					
Bombacaceae	*Quararibea obliquifolia*	Va	6.2	7	7.77	0.388
Fabaceae/Mim.	*Inga thibaudiana*	Va	4.7	10.9	9.11	0.742
Sapotaceae	*Pouteria sp.07*	Va	2.8	8.6	8.9	0.952
Moraceae	*Brosimum alicastrum*	Dg	100	8.3	9.04	0.002
Boraginaceae	*Cordia alliodora*	Dg	100	8.4	9.15	0.002
Tiliaceae	*Goethalsia meiantha*	Dg	73.6	10	9.03	0.004
Sapotaceae	*Pouteria torta*	Dg	69.3	10.3	8.29	0.002
Myristicaceae	*Virola koschnyi*	Dg	55.8	11.8	8.35	0.006
Fabaceae/Caes	*Dialium guianense*	Dg	55	12.7	7.62	0.002
Fabaceae/Caes	*Sclerolobium costaricense*	Dg	53.4	11.2	10.3	0.012
Lauraceae	*Ocotea mollifolia*	Dg	47.2	8.2	9.15	0.026
Fabaceae/Mim.	*Inga paterno*	Dg	46.7	8.2	8.94	0.016
Tiliaceae	*Luehea seemannii*	Dg	46.7	7.7	8.1	0.016
Bignoniaceae	*Tabebuia guayacan*	Dg	45	7.5	7.91	0.018
Anacardiaceae	*Spondias radlkoferi*	Dg	44.1	7.5	7.9	0.018
Anacardiaceae	*Spondias mombin*	Dg	42.8	6.8	6.79	0.012
Meliaceae	*Guarea rhopalocarpa*	Dg	42.5	8.2	8.78	0.028
Lauraceae	*Ocotea ira*	Dg	40.9	8.3	9.58	0.03
Lauraceae	*Ocotea macropoda*	Dg	37.3	7.9	8.56	0.026
Boraginaceae	*Cordia cymosa*	Dg	34.8	8	9.22	0.026
Euphorbiaceae	*Sapium glandulosum*	Dg	34.3	9.2	10.5	0.044
Myristicaceae	*Virola sebifera*	Dg	32.7	11.5	8.67	0.028
Moraceae	*Pseudolmedia spuria*	Dg	29.4	9.9	9.6	0.052
Chrysobalanaceae	*Hirtella media*	Dg	29.3	10.2	10.27	0.066
Tiliaceae	*Apeiba membranacea*	Dg	29.2	12.6	7.95	0.062
Fabaceae/Mim.	*Inga pezizifera*	Dg	27.5	8.9	8.97	0.064
Araliaceae	*Dendropanax arboreus*	Dg	27.1	12.8	8.03	0.06
Cecropiaceae	*Pourouma bicolor*	Dg	27	13.2	8.14	0.07
Euphorbiaceae	*Croton smithianus*	Dg	19.9	10	9.46	0.138
Vochysiaceae	*Vochysia guatemalensis*	Dg	17.3	8.5	9.4	0.11
Rubiaceae	*Chimarrhis parviflora*	Dg	15.2	11	10.09	0.212
Verbenaceae	*Vitex cooperi*	Dg	14.6	10.4	9.49	0.224
Boraginaceae	*Cordia bicolor*	Dg	14.4	11.6	9.66	0.238
Fabaceae/Pap.	*Pterocarpus officinalis*	Dg	13	10.3	9.72	0.236
Apocynaceae	*Lacmellea panamensis*	Dg	12.7	11.1	9.88	0.27

Fabaceae/Mim.	*Inga leiocalycina*	Dg	11.8	10.8	7.71	0.316
Burseraceae	*Protium panamense*	Dg	11.7	11.1	7.73	0.334
Hernandiaceae	*Hernandia didymantha*	Dg	11	11.4	7.86	0.39
Combretaceae	*Terminalia amazonia*	Dg	11	10.9	9.04	0.338

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[1] Dufrêne, M., and Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs, 67:345-66

Appendix 2. Soil sample collection and laboratory analysis.

A single 40cm soil sample was collected from the center of 127, 0.25 ha forest plots with a soil auger. Organic marital was cleared from the top 1 to 2cm of each site previous to collecting a sample. Soil samples were placed in a plastic bag and transported to the soils lab at CATIE in Turrialba, Costa Rica. Each sample was air dried in a screened drying room previous to laboratory analysis. Chemical and physical properties from soils were determined from laboratory analysis for comparisons with tree data from forest plots. Soil pH in water was measured and exchangeable K and P were measured using Modified Olsen extractions with a 0.5 M sodium bicarbonate ($NaHCO_3$) solution at a pH of 8.5 (Olsen and Sommers 1982). Exchangeable Ca, Mg and total acidity extractions were done in a 1N suspension of potassium chloride (KCl) using methods from Diaz Romeu and Hunter (1978). Percent soil organic matter (OM) was measured using the total combustion method following Nelson and Sommer (1996) with pre-treatment to eliminate carbonates. Sand soil texture (percent sand, silt and clay) determined by Bouyoucos method (Bouyoucos 1936). Textural classes were assigned following methods from the USDA Soil Survey Staff (1975).

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Appendix 3. Soil analysis summaries from a 40cm sample taken on 127 forest plots. Results are summarized by a) texture and organic matter and b) chemical properties showing mean and standard deviation by forest types defined in Chapter 1. The order of forest types from the top of the table to bottom generally correspond to increased elevations from ~30m to 1200m above sea level.

a

Forest type	Sand	Silt	Clay	OM
	---------------------------- %	--------------------------------		
Pc	23.9 ± 14.0	19.7 ± 10.6	56.4 ± 16.2	4.6 ± 2.2
Pp	27.2 ± 8.6	16.6 ± 3.7	56.3 ± 9.3	5.9 ± 1.8
Qp	22.5 ± 6.8	16.5 ± 5.7	61.0 ± 7.4	6.3 ± 2.2
Pd	30.8 ± 17.9	17.6 ± 3.6	51.6 ± 17.5	7.3 ± 2.9
Ta	50.3 ± 17.2	19.1± 6.3	30.6 ± 13.5	7.7 ± 2.4
Va	69.5 ± 10.0	14.6 ± 2.9	15.9 ± 9.4	12.5 ± 5.3
Ma	71.8 ± 9.2	14.4 ± 4.2	13.8 ± 7.4	12.1 ± 2.6
Cy	75.3 ± 1.6	15.7 ± 1.5	9.0 ± 3.0	20.6 ± 1.3

b

Forest type	pH	Total acidity	Ca	Mg	K	P
	H_2O	-------------------------	cmol(+)/l	--------------------		mg/l
Pc	4.9 ± 0.7	2.42 ± 1.07	2.35 ± 3.38	1.48 ± 2.17	0.09 ± 0.06	3.94 ± 4.21
Pp	4.5 ± 0.3	3.43 ± 1.26	0.69 ± 1.84	0.37 ± 0.66	0.07± 0.04	2.64 ± 1.31
Qp	4.7 ± 0.4	3.01 ± 0.82	0.41 ± 0.49	0.42 ± 0.31	0.07 ± 0.02	2.91 ± 1.79
Pd	4.5 ± 0.2	3.29 ± 1.00	0.18 ± 0.09	0.23 ± 0.12	0.07 ± 0.02	2.46 ± 0.77
Ta	4.5 ± 0.2	2.69 ± 1.08	0.35 ± 0.45	0.24 ± 0.15	0.09 ± 0.04	2.48 ± 0.99
Va	4.6 ± 0.1	1.81 ± 0.74	0.23 ± 0.15	0.17 ± 0.05	0.10 ± 0.03	2.19 ± 1.07
Ma	4.7 ± 0.3	2.15 ± 1.15	0.49 ± 0.48	0.32 ± 0.21	0.09 ± 0.02	1.87 ± 0.92
Cy	4.6 ± 0.1	1.57 ± 0.54	0.31 ± 0.11	0.21± 0.03	0.12 ± 0.03	2.83 ± 1.04