STRUCTURAL AND FUNCTIONAL CHARACTERISTICS OF TROPICAL SECONDARY FOREST PATCHES IN NORTHEASTERN COSTA RICA

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by

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Authorization to Submit Dissertation

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Abstract

Tropical forests are being threatened by land-use change and deforestation and these activities have created human-modified landscapes of secondary and old-growth forests within a diverse matrix of agricultural uses. We developed an interdisciplinary team project to investigate social-ecological interactions of agricultural intensification in the San Juan-La Selva (SJLS) Biological Corridor in northeastern Costa Rica. This landscape has undergone massive deforestation for conversion to pastures for cattle ranching, and the expansion and intensification of non-traditional exports. Tropical secondary forests are patches of vegetation that regrow naturally in these former pastures. These forests regenerate within this intricate landscape, resulting in patches with complex spatial configurations; albeit the effects of variable landscape configurations on the structure and composition of secondary forests is relatively unknown. In this study, we assessed the relative effects of landscape spatial configuration, environmental variables, forest age and patch spatial location on the structure and composition of seedlings, saplings and trees. Our study was located within the SJLS Biological Corridor, where we established 25, 0.25 ha secondary forest plots located in abandoned pastures, ranging in age from 15 to 55 years post-abandonment. We found that each recruitment stage is affected differentially, with seedling composition mostly affected by soils, while seedling density and diversity were affected by landscape variables. Sapling density and diversity were mostly influenced by landscape configuration while tree species density was influenced by soils. Using six functional traits from 123 species, we analyzed the relative contribution of forest age, spatial location, landscape and environmental factors influencing the functional composition and diversity of sapling assemblages. Functional composition was mostly influenced by soils, while functional diversity was influenced by the plots' spatial location. Leaf dry matter content and leaf nitrogen declined with forest age, while functional divergence increased with forest age. This study highlights the importance of explicitly including landscape spatial configuration as a predictor variable when assessing the structure and composition of tropical secondary forest patches and the need to assess the relative contribution of forest age, spatial location, landscape and environmental variables on each recruitment stage separately.

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Dedication

Para mi esposa Nancy, tu amor, fuerza, motivación y creer en mí en todo momento me han hecho un mejor hombre y una mejor persona. Gracias por toda tu ayuda y por impulsarme a completar este proyecto y todas mis metas. Juntos nada es imposible, te amo mucho.

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Chapter 1: Introduction: The influence of landscape spatial configuration and environmental variables on tropical secondary forest patches

Tropical forests are the world's most biodiverse terrestrial ecosystems (FAO 2015) as they hold two-thirds of all species (Raven 1988) and cover 44% of the world's total forest area (FAO 2015; Keenan *et al.* 2015). They provide a wide range of ecosystem services through the conservation of plant and animal species, hydrological resources, carbon storage, prevention of soil degradation, provision of timber and non-timber products and increase in air quality, while also benefiting the livelihoods of families that depend on forest resources (Brown and Lugo 1990; Finegan 1992; Guariguata and Ostertag 2001; Millennium Ecosystem Assessment 2005; FAO 2015). Constant anthropogenic threats, such as deforestation, land use conversion, climate change and fragmentation of the forest landscape (Chazdon *et al.* 2005) endanger the forest's structural, compositional and functional characteristics and affect all the ecosystem services and benefits provided. As a consequence from these threats, increasing habitat loss has resulted in a decrease of tropical forest area of 195 M ha between 1990 and 2015, with 5.5 M hectares lost from 2010 to 2015 (FAO 2015; Keenan *et al.* 2015). This widespread deforestation has resulted in old-growth forests undergoing extensive conversion to pastures, forest plantations and other agricultural uses (Chazdon 2014). These agricultural areas are sometimes abandoned due to a combination of interrelated factors such as low productivity, human migration patterns associated to shifts from agricultural to industrial economies, changes in social and political policies and expanding urbanization and industrialization (Birdsey and Weaver 1987; Thomlinson *et al.* 1996; Aide *et al.* 2000; Guariguata and Ostertag 2001; Algeet-Abarquero *et al.* 2015). Subsequently, new forests regrow naturally in these abandoned lands surrounded by an agricultural matrix of different uses and old-growth forest remnants (Letcher and Chazdon 2009). These secondary forests are a central fixture in modern tropical landscapes, as by 1990 they were estimated to cover approximately 31% of the total tropical forest cover and now they cover an approximate 60% of the world's remaining tropical forests (Brown and Lugo 1990; Chazdon 2003; FAO 2011; Rozendaal and Chazdon 2015). They are expected to continue to increase in area (Guariguata and Ostertag 2001; Rozendaal and Chazdon 2015).

Constant land use conversion has resulted in an altered landscape spatial configuration of different land uses, as secondary forests regrowing in abandoned agricultural lands (e.g., pastures) exhibit a broad range of patch structural features that characterize their area, edge, shape, and isolation. Landscape spatial configuration can be a determinant of secondary forest structure and composition, especially in the younger recruitment stages, in part because the actual location of the secondary forest patch is determined by topography, distance to old-growth remnants and other secondary patches and distance to roads (Yackulic *et al.* 2011). Topography is an important determinant of the spatial location of both secondary forest patches and old-growth forest remnants, which serve as a crucial seed source, since these tend to be found in marginal agricultural areas of rough terrain, high elevations and steep slopes (Helmer 2000; Asner *et al.* 2009; Rudel 2012; Chazdon 2014). In turn, these areas tend to be of low fertility and production and farther in distance from the road (Helmer 2000; Arroyo-Mora *et al.* 2005). As a result, landscape configuration could possibly affect species composition and structure in secondary forest patches since early colonization and seedling establishment is limited by the hostile environmental conditions present in the early stages of succession (low soil fertility, high solar radiation and high evapotranspiration) and by dispersal limitation, since seed dispersal could be affected by the distance, shape and size of patches and remnants (Finegan 1996; Holl *et al.* 2000; Chazdon 2008; Galanes and Thomlinson 2009; Chazdon *et al.* 2010; Vleut *et al.* 2015). In secondary dry forests of Mexico, Hernández-Stefanoni *et al.* (2011) found that landscape factors related to patch shape and density influenced tree species density. Overall, it is recognized that landscape spatial configuration is a key factor in the determination of species composition and structure, albeit its pure effects on the different recruitment stages are not well understood (Chazdon *et al.* 2007).

Soils and climatic variables can also influence the structure and composition of secondary forest patches, as variation in soil texture and chemical composition can affect forest regeneration, especially in the early stages of succession (Guariguata and Ostertag 2001; Chazdon 2003). Chinea (2002) showed that in secondary forests of eastern Puerto Rico, basal area values were higher and species diversity was lower in alluvial soils when compared to volcanic or plutonic soils. Johnson *et al.* (2000) determined that aboveground biomass accumulation of both tropical and temperate secondary forests was mostly influenced by soil texture (higher in non-sandy soils) and climate (temperature and growing season length). Land use history could also affect soil properties, as secondary forests growing on formers pastures in Puerto Rico showed greater compaction than other land uses, resulting in differing species composition (Aide *et al.* 1995). Forest age also plays a crucial role in the determination of secondary forest characteristics. Usually, species diversity, richness, basal area and above ground biomass increase with forest age (Brown and Lugo 1990; Finegan 1996; Chazdon *et al.* 2007; Rozendaal and Chazdon 2015). As succession proceeds, shade in the understory increases as result of canopy closure, which leads to species turnover and subsequent changes in forest structure (Finegan 1996; Chazdon 2008). Studies suggest that species composition and richness vary independently with forest age (Finegan 1996) and that species composition may take centuries to converge with species composition of mature forests on similar sites, and in some cases does not converge at all (Finegan 1996; Guariguata and Ostertag 2001). However, in the Sarapiquí region of our study area, secondary forest composition is converging with mature forests by recruiting trees and palms of all size classes from mature forests (Norden *et al.* 2009) Consequently, forest age is an important predictor variable for secondary forest structure and composition.

Secondary forests are crucial for our knowledge of community assembly as they provide a good opportunity to investigate the mechanisms by which communities are able to acquire resources under the environmental conditions present in the patch and how they are influenced by the landscape spatial configuration. A suitable approach to understanding secondary forest assembly is by studying the functional properties of young recruitment stages, specifically sapling assemblages. Functional traits are species attributes that influence their survival, growth, reproduction and fitness (Ackerly 2003; Poorter *et al.* 2008) and by studying what factors influence the functional properties of sapling assemblages, we can gain more in-depth knowledge of the mechanistic processes that underlie sapling community regeneration as functional traits are related to species distribution along environmental gradients and forest age (Tilman 1982; Poorter 2007; Lohbeck *et al.* 2012). Niche assembly theory stipulates that environmental conditions and spatial location are the most important variables explaining community assembly; during the initial phases of secondary forest succession it is expected that species will have similar trait values because of shared similarities to adjust to the hostile environmental conditions of early-successional habitats. As succession proceeds, trait values are expected to become more dissimilar because species will tend to have different strategies to out-compete other species (Tilman 1982; Norden *et al.* 2009; Sesnie *et al.* 2009; Letcher *et al.* 2012; Lohbeck *et al.* 2014). Alternatively, dispersal assembly theory stipulates that the ecological processes that are distance dependent, such as seed dispersion from the surrounding metacommunity, have a stronger influence on community assembly than environmental variables, and that the location of any individual is dictated, in part, by the location of the parent tree (Hubbell 2001; Sesnie *et al.* 2009; Rosindell *et al.* 2011). These distance dependent processes have a stronger effect on secondary forest community assembly when the patches are more isolated from seed sources, such as other secondary patches and old-growth remnants (Hubbell 2001; Norden *et al.* 2009; Sesnie *et al.* 2009; Chain-Guadarrama *et al*. 2012; Letcher *et al.* 2012). We asked, what is the relative influence of landscape spatial configuration, environmental variables, forest age and the geographical location of plots on the functional composition and diversity of sapling assemblages? Twenty five, 0.25 ha plots ranging from 15 to 55 years post-abandonment were established in the San Juan La Selva Biological Corridor in northeastern Costa Rica and data was collected on soils physical and chemical properties, climate and landscape spatial configuration metrics to answer the following questions: 1) what is the relative contribution of landscape spatial configuration, environmental variables and forest age on the structure and composition of seedling, saplings and trees? 2) how does landscape, environment and forest age influence sapling assemblages functional composition and diversity?

This dissertation includes two chapters related to the two main disciplinary research questions and one interdisciplinary team-based chapter addressing the social and ecological impacts of agricultural intensification in the study region and its effect on the surrounding forest communities. In Chapter 2, *Effects of landscape spatial configuration and environmental factors on the structure and composition of secondary forest patches in northeastern Costa Rica,* I investigated the relative quantitative effects of landscape configuration, soil physical and chemical properties, climate, geographical location of the plots and forest age on seedling, sapling and tree species density, composition, diversity, and aboveground biomass. Landscape configuration metrics analyzed quantified various attributes at 500 m, 1 km and 5 km radius and measured the isolation (Euclidean distance to other secondary patches and old-growth forest remnants), percent forest cover, edge and shape metrics. Soil samples were taken in each plots and analyzed for texture, pH and chemical properties, while climate variables were taken from the WorldClim data set. Using mixed linear models and variance partitioning statistical methods, I demonstrated that each recruitment stage responds differently to the landscape and environmental variables. There was a negative relationship between seedling diversity and soil sand content, while tree Shannon diversity was positively related to soil pH and sand content. No relationships were found with forest age. Variation in seedling composition was mostly affected by soils, while seedling density was influenced by both climate and landscape configuration. Sapling density and diversity variation was influenced mostly by landscape variables and to a lesser extent the geographical location of plots. Tree species density variation was affected by soils, while tree diversity variation was affected by the geographical location of the plots and by soils. Variation in tree aboveground biomass was influenced by soil properties. Overall, these findings highlight the importance of analyzing each recruitment stage separately and the importance of including landscape spatial configuration as a predictor variable.

In chapter 3, *Functional composition and diversity of sapling assemblages in tropical secondary forest patches and their relationship to landscape spatial configuration and environmental variables*, I explored the relative contribution of forest age, soils, climate, landscape configuration and geographical location of plots influencing sapling assemblages' functional composition and diversity. We sampled six functional traits for 123 species: leaf area, specific leaf area, adult maximum height, leaf dry matter content, leaf nitrogen content and leaf phosphorus content. Functional composition was analyzed as the community weighted means (CWM) for the six traits represented as abundance-weighted mean trait values per plot and functional diversity as a set of four complimentary multi-trait and multidimensional indices. Results indicated that leaf dry matter content and nitrogen declined with forest age, while functional divergence index increased with forest age. Variation in CWM was mostly influenced by soils, while functional diversity indices were influenced by the plots spatial location. This study highlights the importance of the spatial location of secondary forests influencing sapling assemblages' functional diversity and the need to explicitly differentiate between trends in trees and saplings, as shown by the relationships between leaf dry matter content and nitrogen with forest age.

In chapter 4, *Coupled social and ecological outcomes of agricultural intensification in Costa Rica and the future of biodiversity conservation in tropical agricultural regions*, our interdisciplinary team explored the outcomes of pineapple expansion and intensification and their social and economic implications, quantified pineapple' plantations spatial characteristics, their effects on nearby forest communities and the implications for biodiversity conservation in tropical landscapes. Results indicated that pineapple production homogenizes both the agricultural matrix between forest patches and old-growth remnants and the agricultural economy of the region, endangering the biodiversity and the livelihoods of the local small-scale and family producers. We suggested a review of the agricultural and conservation policies to promote heterogeneity in the agricultural and biodiversity sectors by developing land use planning using a landscape level analysis integrating all of the involved stakeholders, from government, pineapple corporations and local producers. This chapter was published in Global Environmental Change 32, 74-86, with Irene Shaver, Adina Chain-Guadarrama, Katherine A. Cleary, Andre Sanfiorenzo, Ricardo J. Santiago-García, Bryan Finegan, Leontina Hormel, Nicole Sibelet, Lee A. Vierling, Nilsa A. Bosque-Pérez, Fabrice DeClerck, Matthew E. Fagan and Lisette P. Waits as coauthors.

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Chapter 2: Effects of landscape spatial configuration and environmental factors on the structure and composition of secondary forest patches in northeastern Costa Rica

Abstract

Tropical secondary forest patches regenerate naturally within a matrix of agriculture and old-growth forest remnants. This complex spatial configuration of forest patches may have an effect on the composition, diversity, density and aboveground biomass of seedlings, saplings and trees, but its influence is not well understood. Through sampling in 25 secondary forest patches, we examined the relative effect of landscape configuration and environmental variables on the composition and structure of the recruitment stages. We found that each recruitment stage is affected differentially, with the variation in seedling composition being more affected by soils, and seedling density and diversity by landscape components. Sapling density and diversity were mostly influenced by landscape configuration while tree density was mostly explained by soils. Seedling density and tree aboveground biomass declined with forest age. Seedlings, saplings and trees are affected in composition and structure by both landscape and environmental variables, highlighting the importance of investigating each recruitment stage separately and how crucial is the landscape spatial configuration influencing tropical secondary forest characteristics.

Introduction

The world's tropical forests are home to approximately two-thirds of all species (Raven 1988) and are the most diverse of all terrestrial ecosystems (Turner and Corlett 1996; FAO 2015). This great concentration of biodiversity is threatened worldwide by land use change and habitat loss, widely recognized as major threats (Novacek and Cleland 2001; Arroyo-Rodríguez *et al.* 2013). Global deforestation is occurring mainly in the tropics, with 195 million hectares (ha) lost between 1990 and 2015, with a net rate loss of forest area of 5.5 million ha annually from 2010-2015 (FAO 2015; Keenan *et al.* 2015). Deforestation not only represents a threat to biodiversity, but also to ecosystem function, processes and human welfare (Millennium Ecosystem Assessment 2005; Carrara *et al.* 2015).

Extensive land use changes alter landscape spatial configuration, as some agricultural lands (e.g., pastures) are abandoned and new forest regrows. Secondary forest patches regenerate through natural processes after the complete removal of the original forest cover. In these tropical agricultural landscapes, secondary forest patches emerge within a matrix of surrounding old-growth forest remnants and agricultural lands (Letcher and Chazdon 2009), as continuous tracts of forest are divided due to agricultural expansion, illegal logging, and human population growth (Laurance 1999; FAO 2011; Arroyo-Rodríguez *et al.* 2013; Laurance *et al.* 2014). The fragmentation of continuous areas of natural habitat due to expanding agricultural or urban use (Bennett 1998; Fahrig 2003) not only affects the spatial configuration of secondary forest patches, but also changes the physical characteristics of the surrounding land uses, with each patch having a particular size, shape and distance to other patches.

The variation in patch structural characteristics of secondary forests (e.g., patch area, shape, surrounding forest cover and the distance between secondary patches and old-growth fragments) could possibly influence the composition, richness and structure of these patches since the ecological processes that control them may be regulated at a landscape scale (Turner 1989; de Blois *et al.* 2002; Opdam *et al.* 2003; Galanes and Thomlinson 2009; Vleut *et al.* 2015). In secondary forests, initial colonization and seedling recruitment are often dispersal limited (Holl *et al.* 2000; Cubiña and Aide 2001; Dalling and Hubbell 2002; Chazdon *et al.* 2010) as spatial patterns of seed dispersal and the eventual establishment and distribution of plant species can be affected in part by the size, shape and connectivity to nearby patches and fragments that serve as seed sources (Turner 1989; Galanes and Thomlinson 2009; Vleut *et al.* 2015). Moreover, alteration of the dispersal process occurs because changes in landscape spatial configuration increase the isolation or distance between patches and fragments, affecting frugivorous bat and bird communities that are responsible for seed dispersal, since seeds of most woody species in neotropical lowlands are dispersed by vertebrates (Finegan 1996; Melo *et al.* 2006; Cramer *et al.* 2007; Zamora *et al.* 2010; Vleut *et al.* 2012; Arroyo-Rodríguez *et al.* 2013; Vleut *et al.* 2015). Secondary forest patches and old-growth forests provide suitable habitat for roosting and feeding bats and for habitat-generalist and forest-specialist bird species, but also serve as seed sources from which bats disperse a range of early-successional to mid- and late-successional large seed species, contributing to the succession of these forests (Blake and Loiselle 2001; Melo *et al.* 2009; Saldaña-Vazquez *et al.* 2010; Vleut *et al.* 2015).

Changes in landscape spatial configuration could have effects on secondary forest patches similar to old-growth fragments, even though secondary forests exhibit differences in structure and composition with respect to nearby old-growth forests on similar site conditions

(Finegan 1996; Guariguata *et al.* 1997; Chokkalingam and De Jong 2001; Guariguata and Ostertag 2001; Santo-Silva *et al.* 2013). Species composition will typically increase with distance between old-growth fragments due to a combination of seed dispersal limitation and variation in environmental conditions (Hubbell 2001; Arroyo-Rodríguez *et al.* 2013), however the effect of the spatial context on secondary forest patches is not well understood (Chazdon *et al.* 2007). Time of abandonment or patch age is also an important factor in the determination of secondary forest characteristics. Studies suggest that species richness, species density, canopy height and aboveground biomass will increase as the time of abandonment increases (Brown and Lugo 1990; Aide *et al.* 1996; Finegan 1996; van Breugel *et al.* 2006; Chazdon *et al.* 2007; Rozendaal and Chazdon 2015). However, variation exists in forest community structure and composition between patches of similar age (Guariguata *et al.* 1997; Finegan and Delgado 2000; van Breugel *et al.* 2006; Chazdon *et al.* 2007). Relating this variation in structure and composition with the landscape spatial configuration and environmental factors will give us a better understanding of secondary forest community assembly.

Environmental variables also play an important role in the determination of secondary forest composition and structure, however their importance, relative to old-growth forests, is not well characterized (Dent and Wright 2009). For example, differences in microhabitats and variations in soil nutrients influence composition, distribution and growth of species, especially during the early stages of secondary succession (Uhl *et al.* 1982; Guariguata and Ostertag 2001). In old-growth forests remnants of northeastern Costa Rica, variation in forest composition has been reported following strong spatial patterns that vary along geographical and environmental distance, with significant spatial autocorrelation for species composition and environmental variables up to 13 km distance (Sesnie *et al*. 2009). However, after controlling for environmental variables, Sesnie *et al*. (2009) did no find a strong relationship between tree and palm abundance and geographical distance. For both trees and palms, variation in species composition was significantly correlated to soil organic matter, sand and clay, while palm abundance was significantly correlated to Ca, Mg, pH and total acidity (Sesnie *et al.* 2009), demonstrating the effect of environmental variables on species composition of old-growth forest remnants. Our work was performed in secondary forest patches in the same landscape, and we asked whether we would find similar results. Alternatively, since these patches are by definition, not continuous, we asked if spatial variables would have a greater influence than environmental variables in determining the structure and composition of secondary forest patches.

The relative impact of both landscape spatial configuration and environmental variables on the composition and structure of tropical secondary forest patches is not well known, as it is difficult to quantify (Chazdon *et al.* 2007; Karp *et al.* 2012). Additionally, most studies of forest variation over landscapes within agricultural matrices do not consider the independent effects of landscape configuration on composition, richness, and diversity of seedlings, saplings and trees, as they tend to focus on one particular recruitment stage and are mostly done at the patch level with old-growth fragments (Benítez-Malvido and Martínez-Ramos 2003; Hernández-Stefanoni 2006; Galanes and Thomlinson 2009; Carrara *et al.* 2015). Ultimately, and depending on the spatial and temporal scales studied, a combination of seed dispersal limitation and the site's environmental and geographical conditions, previous land uses, species biology, and its interaction with other species influences forest's species composition and structure (Guariguata and Ostertag 2001; Hubbell 2001; Austin 2002; Chazdon 2008; Norden *et al.* 2009; Sesnie *et al.* 2009). In this study, we sought to quantify the relative importance of landscape configuration and environmental variables determining the composition, aboveground biomass, diversity and species density of seedlings, saplings and trees in secondary forest patches within an agricultural landscape in northeastern Costa Rica. Our specific objectives were to: 1) quantify landscape and environmental differences between secondary forest patches, 2) evaluate species composition, aboveground biomass, diversity and density of the three recruitment stages, and 3) determine the degree of contribution of landscape and environmental variables to the observed variation in seedling, sapling and tree composition, aboveground biomass, diversity and species density. We hypothesized that landscape spatial configuration and environmental variables will affect each recruitment stage differentially because each stage has a different mechanistic process that regulates them. Seedlings and saplings may be more strongly influenced by landscape factors because of probable seed dispersion limitation (Hubbell 2001; Guariguata and Ostertag 2001), while trees may be more strongly affected by environmental variables, which have been shown to influence species composition in old-growth forests in our landscape (Sesnie *et al.* 2009).

Methods

Study Area

The study area is located within the San Juan-La Selva (SJLS) Biological Corridor in northeastern Costa Rica (Figure Ch2-1). Located between the Sarapiquí and San Carlos counties in the provinces of Heredia and Alajuela, respectively, the SJLS corridor was established in 2001 as part of the Mesoamerican Biological Corridor, with the purpose of maintaining connectivity between the Indio-Maíz Reserve in southeastern Nicaragua and the northern part of Costa Rica in the Área de Conservación Arenal Huetar Norte and the Área de Conservación de la Cordillera Volcánica Central (Villate *et al.* 2009). It has an area of 245,008 ha, which by 2011 had 58.5% forest cover (47.2% old-growth forest, and 11.3% secondary forests, including native tree plantations) and an agricultural matrix mainly consisting of pasture, which covers an area of 32% and pineapple with 2.0% (Shaver *et al.* 2015).

The forests are classified in the Holdridge Life Zone as wet tropical forest (Tosi 1969; Holdridge *et al.* 1975). Elevation ranges from sea level to 3,000 m in the Central Volcanic Range (Lieberman *et al.* 1996). Mean annual precipitation ranges from 3,000 mm in the western lowlands to 4,500 mm in the foothills (Grieve *et al.* 1990; Sesnie *et al.* 2009). The eastern and southern areas of the Corridor receive ≥ 150 mm of monthly precipitation throughout the year and the western and northern areas of the Corridor average < 100 mm of rainfall during the driest month (Sesnie *et al.* 2009). Mean annual temperatures average near 24°C in the lowlands (Lieberman *et al.* 1996). The topography of the landscape is characterized by terraces, lowland alluvial flood plains, low hills and mountain slopes with steep ravines in upper elevation areas (Sesnie *et al.* 2009). Soils are very acidic (pH~4) Inceptisols derived from colluvial and alluvial deposits and Ultisols derived from andesitic material with sandy clay textures of late Tertiary and Quaternary origin, with development and soil age varying depending on distance from volcanoes, lava flows, and ash falls (Sollins *et al.* 1994).

In the SJLS Corridor, secondary forests are smaller, more isolated and subdivided than old-growth forests (Shaver *et al.* 2015). Mean patch area is only 6 ha, with its largest patch (Largest Patch Index-LPI) covering only 0.14 % of the landscape compared to a mean patch area of 76 ha for old-growth forests and its LPI covering 13.7% of the landscape. Secondary forest patches have an average distance (isolation quantified as Euclidean Nearest Neighbor-ENN) between patches of 142 m while old-growth forests have an average ENN of 121 m between remnants. Mean ENN between secondary and old-growth forest is 1,139 m. The number of patches for secondary forests is estimated to be 4,628 while for old-growth forest is estimated at 1,529 remnants (Shaver *et al.* 2015).

Site Selection, Plot Establishment and Measurements

We established 25, 0.25 ha (50 x 50 m) plots across the Corridor (Figure Ch2-1). The Corridor was divided into three landscapes, and we established 16 plots in landscape 1, 4 in landscape 2 and 5 in landscape 3. Landscapes were differentiated by their surrounding forest covers at a 6 km radius, with landscape 1 having 50%, landscape 2 with 65% and landscape 3 with 71% forest cover. Plots were georeferenced using a GPS and digitized into land use maps. They ranged in elevation between 0 and 280 masl. All plots were established in former pastures and areas that were cleared but not used and ranged between 26-55 years post-abandonment. Age of abandonment was obtained from information provided by each landowner and verified using land use maps. We established a 10 m edge from the pasture to the inside of the forest and a minimum distance of 300 m between plots. In each plot, we measured diameter at breast height (dbh-1.3m) and identified every stem $\geq$ 5 cm dbh for each individual tree, palm, and arboreal fern and 0.5 cm dbh for lianas. We established three 50 × 5 m transects to measure and identify saplings between 1 to 4.9 cm dbh and three 50 × 2 m transects to count and identify seedlings < 1 cm dbh (Norden *et al.* 2009). Transects were separated by 10 m, alternated between seedlings and saplings. Species were identified in the field by a parataxonomist (Marvin Zamora or Vicente Herra), and unknown species were assigned a code for morphospecies.

Around each plot center, we calculated 15 landscape configuration variables within a 500 m, 1 km and 5 km radius using the 2011 land use map developed by Shaver *et al.* (2015). The metrics quantified the total area of secondary forest, percent forest cover of secondary forest, percent forest cover of mature forest, number of patches, patch density, largest patch index, total edge, edge density, mean patch area, patch shape index, perimeter to area ratio, ENN between secondary patches, ENN between secondary forest patches and mature forests, aggregation and clumpiness indices. Metrics were calculated with Fragstats 4.2 (McGarigal *et al.* 2012). A digital elevation model (DEM) was used to obtain plot elevations and percent slope was estimated from the DEM using ArcMap 9.3. We obtained 19 bioclimatic variables from WorldClim (http://www.worldclim.org). This is a bioclimatic data set with 30 arc-second grids and 1 km^2 spatial resolution. To evaluate soil physical and chemical properties, we collected 5 samples in each plot representing the 0-40 cm depth, one in each corner and one at the plot center, with organic material cleared from the first 2 cm prior to auguring (Sesnie *et al.* 2009) and latter combined to make a homogeneous sample per plot. We placed the samples in labeled plastic bags and air-dried them prior to analysis. The soils laboratory of the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE- Turrialba, Costa Rica) analyzed the soil samples for each plot for pH, extractable K, P, Ca, Cu, Zn, Mn, Fe, Mg, percent N, percent C, and total acidity (indicator of potential aluminum toxicity). These properties are believed to affect forest composition and tree growth (Sollins 1998, Sesnie *et al.* 2009). Cu, Zn, Mn, Fe, K and P extractions were measured using Modified Olsen extraction at a pH of 8.5. Total acidity, Ca, and Mg extractions were done using potassium chloride (KCl), soil pH in water and N and C by combustion in an autoanalyzing equipment. Soil texture (% sand, silt and clay) were determined using the Bouyoucos method and textural classes were assigned following USDA Soil survey standards. Textural properties are indicators of water retention and drainage and they may affect tree species distributions (Sollins *et al.* 1994, Sollins 1998).

Data Analysis

For each recruitment stage, composition (measured on the basis of the abundance of each species), species density, and Shannon diversity index were calculated. We calculated tree aboveground biomass (AGB) using the allometric equation proposed by van Breugel *et al.* (2011) as a multispecies model based on their dbh: ln(AGB)= -1.863+2.208 * ln dbh. The back-transformed AGB value was multiplied by the correction factor of 1.1. For species with a dbh $\geq$ 25 cm, we used a general equation developed by Brown (1997) for wet tropical forests. We excluded remnants trees, palms, lianas and tree ferns in the AGB calculations. We subjectively identified these remnant trees on the basis of very large size and species identification, i.e. species like *Minquartia guianensis* grow very slowly and are scarce among trees in secondary forests in this landscape (R. Santiago and B. Finegan personal observation; Finegan *et al.* 1999;

Chazdon *et al.* 2011). Species density was calculated as the number of species found in each plot for each recruitment stage. Species diversity was analyzed using the Shannon Index. We performed these analyses using the InfoStat statistical package (InfoStat 2014, Di Rienzo *et al.* 2014). To understand patterns of environmental variation across a landscape, we used Pearson correlations to determine if significant relationships existed between soil, climate and landscape variables ($P<0.05$). We performed cluster analysis using the Ward method (minimum variance method) and Bray-Curtis distance to measure similarity or dissimilarity in the composition data for each recruitment stage and grouped the plots accordingly. The cluster analysis groups plots based on the species abundances and is used "a priori" to obtain a better understanding of the structure of the data. Nonmetric Multidimensional Scaling (NMS) was used to characterize floristic composition in each plot for each recruitment stage using the QEco software (Di Rienzo *et al.* 2010). Forty runs with real data and 50 runs with randomized data were used to assess the stability of the final ordination, considering only species recorded in two or more plots (Greig-Smith 1983). Geographical distances between plots were log transformed to estimate the effects of random species dispersal (Hubbell 2001). We determined the effects of plot age on composition for each recruitment stage by plotting plot age against the eigenvector values obtained from each axis of the NMS ordinations and conducted Pearson correlations between these values. These analyses were done using the InfoStat software.

Principal components analysis (PCA) was used with the soils, climate and landscape data to find a new set of uncorrelated variables that explain the structure of the variability in the data. It identified the main soils, climate and landscape gradients along the sampled plots. To select the variables used to test relationships between diversity and species density of each recruitment stage, we chose the eigenvalues from the PCA that explained approximately 90% of the variation in the data. Afterwards, we did Pearson correlations with the eigenvectors to see which variables had positive or negative correlations and these variables were used to run the analyses. We used mixed linear models (MLMs) since the residuals for each model presented a normal distribution. MLMs quantify the relationship between several predictor variables and a single dependent continuous variable, using a least square regression approach. An advantage of using MLMs is the possibility to include plot coordinates as covariates to take into account spatial correlations; in our study we used the planar coordinates (CRTM05) of the study plots to address the issue of lack of spatial independence. For each recruitment stage we ran the analysis using the most parsimonious models, by utilizing a backward elimination procedure. We also used MLMs to test for the effect of forest age on species density and diversity for each recruitment stage.

To test the relative contribution of landscape and environmental variables to the variation in composition and structure of recruitment stages, we performed a variation partition analysis (Borcard *et al.* 1992; Legendre 2008) on each recruitment stage for composition, diversity and species density and for tree aboveground biomass. The analysis partitions the variation of species composition, diversity, aboveground biomass and species density into the contributions of soils, climate, landscape and space. Geographical plot coordinates were transformed using logarithmic transformation and Euclidean distances, by generating a matrix of geographical distances between plots using principal coordinates of neighbor matrices (PCNM) analysis (Borcard *et al.* 2002). This allows the representation of the spatial component using positive eigenvalues as spatial predictors. We evaluated the correlations between landscapes variables and the PCNM's by running Pearson correlations. Species abundances were transformed using a Hellinger transformation before the analysis to downweight the most abundant species. A forward selection process (Jones *et al.* 2008; Legendre *et al.* 2009) was run for each set of variables (soils, climate, landscape and space) for each recruitment stage. This procedure selects the variables that go into the variation partition analysis and are those who have a significant contribution ($P<0.05$, 999 random permutations) to explain the observed variation in abundance, diversity and richness and aboveground biomass. Adjusted R^2, F and P ($P<0.05$) values are reported for each set of predictor variables for each recruitment stage. We performed these analyses using the QEco statistical package.

Results

Soil and climate gradients

Soils were very strongly acidic (mean pH 4.23 ± 0.19) sandy clay loam (Table Ch2-1). Principal component analyses (Appendix 1a) show the first axis representing a gradient in sand, nitrogen and carbon content, with 28.9% of the variation explained. Sand composed more than half of the soil particles while having the highest standard deviation (52.2 ± 12.48) (Table Ch2-

1). Soils with a high percentage of sand were positively associated with Fe, percent C and N and negatively associated with pH. Axis 2, explaining 20% of the variation, represented a gradient of cation concentrations (Ca, Mg, K) along with Mn and Zn. Significantly positive Pearson correlations were observed between pH and K, P, Zn, C and Mn to a lesser degree, indicating a relationship between acidity and soil fertility.

The majority of the climatic variables did not show noticeable ranges between plots, with precipitation values having more variation than temperature (Table Ch2-1). Annual precipitation had the most variation, reflected in the differences between the northern and southern areas of the region (Appendix 1b). When looking at individual plot values, minimum monthly precipitation and precipitation seasonality reflect this gradient of precipitation, with plots in the southern area having higher minimum monthly precipitation and less precipitation seasonality. The elevation range of plots (0-280 masl) had the most variation of the terrain variables and had the expected strong negative correlation with annual mean temperature (Pearson $r = -0.94$, $P < 0.0001$) and precipitation seasonality (Pearson $r = -0.63$, $P < 0.0007$) and positive correlations with mean diurnal range (Pearson $r = 0.86$, $P < 0.0001$) and temperature annual range (Pearson $r = 0.80$, $P < 0.0001$). Slope was not strongly correlated with any of the climatic variables.

Landscape metrics

Landscape variables exhibited an extensive range of values, due to the fact that measurements were made at various radii for every plot (Appendix 1c, 1d, 1e). Two plots were excluded from the analysis at 1 km and at 5 km radii because they are located close to the San Juan River and the border with Nicaragua, and the radii extended beyond the study area where we do not have data. Isolation (ENN) between secondary patches was highest at the 5 km radii with a mean distance of 150.2 m and lowest at 83.4 m within the 500 m radius. Between secondary and mature forests, the highest distance was 3,071.2 m at 5 km and the lowest distance was 25.3 m at 500 m. Secondary forest cover was highest at 500 m with 18.2% while the highest mature forest cover was only 0.48% also at 500 m. Secondary forest patches edge density was lowest at 5 km with 28.43 m/ha and highest at 500 m with 54.53 m/ha. Mean patch area averaged 4.13 ha at 5 km, 5.33 ha at 1 km and 5.41 at 500 m, while patch density (number of patches/area) averaged 3.29 at 5 km, 3.17 at 1 km and 4.65 at 500 m. The mean percentage of secondary forest cover was greater at 500 m (18.2%) and lowest at 5 km (9.55%), while mean mature forest cover at all radii was low, not reaching 1%.

Forest community composition

We encountered a total of 372 plant species in all plots among all recruitment stages (6,083 individuals), comprising 202 genera. Seventy-nine percent were identified to the species level; the remaining were assigned to genus (16%) or morphospecies level (5%). Tree species accounted for 96.4% of individuals sampled while the remaining species were palms (2.6%), lianas (0.5%), and arboreal ferns (0.5%).

Seedlings

We found 246 species of seedlings, representing 2,342 individuals. Of these, 95.2% were tree species, 4% palms, 0.4% lianas and 0.4% arboreal ferns. Eighty-one percent were identified to species level, 18% to the genus level and 1% remained unknown morphospecies. The most abundant seedling species was *Psychotria suerrensis* (Rubiaceae) with 1,172 individuals. Cluster analysis did not separate plots into clearly distinct groups (Figure Ch2-2a), indicating that seedling abundance distribution among plots is similar. We performed an NMS analysis with information from 204 species recorded in two or more plots. This produced a three-dimensional solution (Figure Ch2-3a), with a final stress index of 18.59. Axes 1, 2 and 3 respectively, explained 23.4%, 22.7%, and 19.9% of floristic variation among plots, for a total of 66% of explained variation. The ordination shows the continuum of seedling species composition in a multivariate space based on their abundance along the plots and a tendency to form two groups on axis 1. The grouping consists of 14 plots with positive axis 1 scores, and contains 9 of the 16 plots in landscape 1, 1 of the 4 plots from landscape 2 and 4 of the 5 plots in landscape 3. The other group was mainly made up of plots from landscape 1 and three of the four from landscape 2. The species in the center of the figure, *Pentaclethra macroloba*, *Enterolobium schomburgkii* and *Stemmadenia robinsonii*, are not associated with any particular plot as their abundances indicate that they can be found along the continuum of species composition. Plot age was positively correlated with the first axis of the ordination (r = 0.41, P

= 0.0427). The positive correlation between age of abandonment and the first axis of NMS is an indication of beta diversity, or seedling species turnover.

Axis 1 presented strong positive correlations with *Chimarrhis parviflora* (r = 0.39), *Clethra costaricensis* (r = 0.56), *Inga* sp. 1 (r = 0.52), *Inga* sp. 2 (r = 0.46), *Talisia nervosa* (r = 0.34), *Vatairea lundellii* (r = 0.34), and *Vantanea barbourii* (r = 0.65), so that these are the species associated with the first group of plots. Negative correlations were found with *Guarea bullata* (r = -0.76), *Inga sertulifera* (r = -0.40), *Lacmellea panamensis* (r = -0.49), *Piper colubrinum* (r = -0.78), *P. suerrensis (*r = -0.56*)*, *Dystovomita* sp. *(*r = -0.76*)*, and *Vouarana anomala* (r = -0.76), thus, these are the species associated with the second group of plots. Axis 2 presented positive correlations with *Cespedesia spathulata* (r = 0.62), *Inga cocleensis* (r = 0.54), *Minquartia guianensis* (r = 0.57), *P. macroloba* (r = 0.70), *Psychotria panamensis* (r = 0.52), and negative correlations with *Dussia macroprophyllata* (r = -0.40), *Guatteria diospyroides* (r = -0.61), *Hirtella triandra* (r = -0.42), *Pouteria durlandii* (r = -0.53), *Protium schippii* (r = -0.56), *Stemmadenia robinsonii* (r = -0.40) and *Virola koschnyi* (r = -0.57).

Saplings

For saplings, we recorded 279 species, comprising 1,970 individuals. Among these, 95.9% were canopy tree species, 3% palms, 0.4% lianas and 0.7% arboreal ferns. Eighty-four percent were identified to species level, 15% to the genus level and 1% remained unknown morphospecies. The most abundant sapling species was *Casearia arborea* (Salicaceae) with 236 individuals. Cluster analysis indicated the formation of three groups along axis 1 (Figure Ch2-2b). One of the groups has plots from landscape 2 and 3, a second group has only plots from landscape 1 and the third group has plots from landscape 1 and two plots from landscape 3. Sapling composition was more similar between plots in landscapes 2 and 3, while plots in landscape 1 were more similar between each other. The NMS analysis (Figure Ch2-3b), performed with 227 species recorded in two or more plots, had a final stress index of 16.26. Axes 1, 2 and 3 respectively explained 28.1%, 25.2% and 22.7% of floristic variation among plots, for a total of 76% of explained variation. The ordinations show a separation of three groups of plots along the plot distributions. The first group has 12 plots with positive axis 1 scores and contains 6 plots from landscape 1, 2 plots from landscape 2 and 4 plots from landscape 3. The second group consists of 7 plots with negative axis 1 scores and contains 4 plots from landscape 1, 2 plots from landscape 2 and 1 from landscape 3. The third group contains 6 plots from landscape 1, all with negative scores from axis 1. Species in the center of the figure, *Pouteria torta*, *Balizia elegans*, *P. macroloba*, and *V. lundellii* are not associated with any particular plot. Plot coordinates on axis 1 presented strong positive correlations with *Alibertia atlantica* (r = 0.68), *Ferdinandusa panamensis* (r = 0.54), *Guatteria aeruginosa* (r = 0.50), *L. panamensis* (r = 0.50), *Psychotria elata* (r = 0.58), and *Stenama spruceii* (r = 0.41), these species are associated with the first group of plots. Negative correlations were found with *Carpotroche platyptera* (r = -0.52), *Dendropanax arboreus* (r = -0.52), *Parathesis trichogyne* (r = -0.53) and *V. koschnyi* (r= -0.48), and these species were associated with the second group of plots. Axis 2 presented strong positive correlations with *G. diospyroides* (r = 0.42), *Hernandia stenura* (r = 0.41), *Lecuentea amazonica* (r = 0.41), *P. colubrinum* (r = 0.60), and *Siparuna* sp. (r = 0.44) and strong negative relationships with *Calophyllum brasiliense* (r = -0.59), *Faramea occidentalis* (r = -0.49), *H. triandra* (r = -0.59), *Maranthes panamensis* (r = -0.51), *Minquartia guianensis* (r = -0.55), and *Naucleopsis naga* (r= -0*.63).*

Trees

We found 268 tree species, with a total of 1,771 individuals. Of these, 97% were tree species, 2% palms, 0.3% lianas and 0.7% arboreal ferns. Eighty-five percent were identified to species level, 14% to the genus level and 1% remained unknown morphospecies. Within the adult height categories, we found 3% for understory species, 48% for middle story species, 26% for canopy species and 23% for emergent species. The most abundant tree species, as in the case with saplings, was *C. arborea* with 612 individuals. Cluster analysis (Figure Ch2-2c) shows three groups of tree species. One group has species from landscape 1 only, while the other two groups have a mix of the three landscapes. Even though these three groups differentiated, the fact that the groups have a mix of plots from the three landscapes shows that the abundance of tree species is not distinguishable by landscapes. The NMS analysis (Figure Ch2-3c), performed with 253 species recorded in two or more plots, had a final stress index of 13.48. Axes 1, 2 and 3 respectively explained 37.8%, 24.3% and 23.9% of floristic variation among plots, for a total of 86% of explained variation. Three groups appear in the ordination, however they are less clearly distinguished compared to seedling or saplings. Ten plots from landscape 1 have negative values on axis 1, while all the plots from landscapes 2 and 3, with some plots from landscape 1, have positive values. Plot 25 appears to be an outlier in this ordination, with *Couma macrocarpa* presenting a strong association with this plot. Axis 1 presented strong positive correlations with *C. arborea* (r = 0.59), *Cordia dwyeri* (r = 0.45), *Lonchocarpus oliganthus* (r = 0.48), the liana *Pinzona coriacea* (r = 0.52), *Trichospermum grewiifolium* (r = 0.32), and *Unonopsis pittieri* (r = 0.45), thus, these are the species most associated with landscapes 2 and 3. Negative relationships with *Ardisia fimbrillifera* (r = -0.56), the palm *Bactris* sp. (r = -0.66), *Bauhinia guianensis* (r = -0.59), *Castilla elastica* (r = -0.61), *Dipteryx panamensis* (r = -0.55), *Gmelina arborea* (r = -0.61), *Humiriastrum diguense* (r = -0.51), *Inga chocoensis* (r = -0.63), *Luehea seemannii* (r = -0.66), and *Miconia ampla* (r = -0.62) showed that these are the species most associated with landscape 1. Axis 2 presented positive correlations with *Apeiba membranacea* (r = 0.32), *C. arborea* (r =0.36), *Colubrina spinosa* (r = 0.40), *Goethalsia meiantha* (r = 0.60), *Cecropia obtusifolia* (r = 0.25), *Paullinia granatensis* (r = 0.33), *Tetracera portobellensis* (r = 0.30), and *Virola sebifera* (r = 0.32), and strong negative correlations with *A. atlantica* (r = -0.50), *C. macrocarpa* (r = -0.48), *Cupania glabra* (r = -0.57), *F. panamensis* (r = -0.59), *H. triandra* (r = -0.58), *Protium pittieri* (r = -0.58), *Tetragastris panamensis* (r = -0.63), and *Vochysia ferruginea* (r = -0.56). Tree aboveground biomass averaged 104.32 Mg/ha for 24 secondary forest plots. We excluded one plot from the analysis because it contained remnant individuals of planted *Pinus caribaea*. We found a median value of 98.1 Mg/ha, while the lowest value was 47.89 Mg/ha and the maximum value was 185.06 Mg/ha (Table Ch2-2). Plots in landscape 1 had higher average aboveground biomass values (120.67 Mg/ha), while landscape 3 had the lowest average values (75.5 Mg/ha).

Relationships of recruitment stages with forest age, environmental and landscape variables

We excluded the temperature variables from the WorldClim dataset because there was little variation for the data in our plots and detecting any relationships was thus, not possible. These were excluded from all the MLMs analyses for all recruitment stages. We found no relationship between seedling species density, diversity and forest age. No relationships were found between seedling species density and soil, climate or landscape variables. Soil physical properties affected seedling Shannon diversity, as there was a negative relationship between seedling diversity and soil sand content (R^2: 0.26, p: 0.0088) (Figure Ch2-4). No relationships were found for climatic and landscape variables. For saplings, we found no relationships between species density and diversity and any of the predictor variables, including forest age. We found no relationships with forest age, soil, climatic or landscape variables and tree species density. Tree Shannon diversity was positively related to soil pH (R^2: 0.42, p: 0.0083) and sand content (R^2: 0.42, p: 0.0021). No other significant relationship was found between tree diversity and climatic, landscape variables or forest age. We did not find any relationship between tree aboveground biomass and forest age.

Variance partitioning

Composition

For seedlings, the forward selection procedure retained two principal coordinates of neighbor matrices (PCNMs) for modeling composition, PCNM 1 and PCNM 21. The final soil components related to the overall seedling composition included sand, K, Cu, and Fe, the climate component included precipitation seasonality, and the landscape component was the aggregation index at 1 km radius. The variance partitioning showed that soils, climate, landscape and space explained 31% of variation of the overall seedling species composition, while 69% remained unexplained (Table Ch2-3a). Soils explained more the variation in seedling species composition in comparison with climate, landscape and space. These results are further confirmed when observing the significant pure effects of soils when controlling for the effects of the other three variables, indicating that in this landscape, textural and chemical soil properties are the most important factors controlling for seedling species composition.

For saplings, the forward selection retained eight PCNMs: 1, 2, 3, 9, 10, 16, 19, and 21. The soil component related to the overall sapling composition included Mn, Mg, Cu, Ca, acidity, and pH, the climate component included precipitation of the warmest quarter, and the landscape component included mature forest cover at 5 km, and mean patch area for secondary forests for 1 km and 500 m. Soils, climate, landscape and space explained 25% of the variation in overall sapling species composition, while 75% remained unexplained (Table Ch2-3a). All four components were significantly related to saplings composition, with space explaining more the variation than soils, climate and landscape.

For trees, the forward selection retained four PCNMs: 1, 2, 21 and 22. The soil components were sand, pH, Cu, Fe, and K, the climate component was precipitation of the warmest quarter, and the landscape components were perimeter to area ratio at 1 km, mature forest cover at 5 km, secondary forest area at 500 m, and distance between secondary and mature forest at 1 km. Variance partitioning showed that soils, climate, landscape and space were related to 22% of variation of the overall tree species composition, while 78% remained unexplained (Table Ch2-3a). The four components were significantly related to tree composition, with soils and space explaining more the variation; however no independent signal from any of the variables could be detected.

Species density

The seedlings species density forward selection procedure retained two PCNMs, 16 and 20. Sand was selected as the soils component, precipitation of wettest month was selected for climate and the landscape components selected were perimeter to area ratio at 5 km, aggregation index for 1 km and ENN between secondary forests at 500 m. Variance partitioning (Table Ch2-3b) showed that all four components combined explained 73% of the observed variation in seedling richness, while 27% remained unexplained. Landscape and climate components explained the most variation in seedling density. When observing the pure effects of all components, landscape and climate remain the strongest factors, with landscape explaining most of the variation in seedling density. The landscape components chosen at different radii probably imply that at a closer distance, distance between secondary forests may be playing an important role in dispersal and at 1 km radius the frequency by which pairs of secondary forest patches appear together in the landscape might indicate that this source of nearby propagules is needed to maintain seedling density. Perimeter-to-area ratio can be an indicator of the importance of patch shape.

Sapling species density forward procedure selected two PCNMs: 14 and 16. No soils and climate components were chosen from the forward selection, indicating that they are not important drivers of the observed variation of sapling species density. The landscape components selected were the clumpiness index at 5 km and the aggregation index and mean patch area at 500 m radius. These components together explained 59% of sapling richness variation, while 41% remained unexplained (Table Ch2-3b). Landscape components explained more of the variation than PCNM's, and the pure effects indicate that the landscape is exerting a greater influence in sapling richness. For tree species density, the three PCNMs selected were 5, 13 and 16. The forward selection selected the soils properties pH, Fe and Mn, for the climate component it was isothermality and mean diurnal range of temperature and for landscape it was aggregation index for 500 m and 1 km. The combined components explained 65% of variation, while 35% of the variation remained unexplained (Table Ch2-3b). All components were significantly related to tree richness, with soils explaining most of the variation, along with the landscape component.

Diversity

Seedling forward selection did not select any PCNM, climate or landscape components. Soil components selected were sand and Zn. Since only one component was chosen in the forward selection, the variance partitioning was not performed. The sapling forward selection for the spatial component chose PCNM 4, while the landscape component was the shape index at 1 km radius. Both components explained 46% of the sapling diversity, while 54% remained unexplained (Table Ch2-3c). The shape index explained most of the variation in sapling diversity. Tree diversity forward selection retained three principal coordinates of neighbor matrices for modeling diversity variation, 2, 7, and 21. The soil component included sand and pH, the climate component was mean temperature of wettest quarter, and for landscape it was aggregation index for 1 km. Variance partitioning (Table Ch2-3c) showed that all components were significantly related to tree diversity, explaining 71% of the variation, with space and soils being the strongest components. However, after controlling for the effects of the other variables, soils remained significant.

Aboveground biomass

The forward selection procedure selected PCNMs 2 and 3, K and Cu for the soils variables, precipitation seasonality and precipitation of the warmest quarter for climate and for landscape it selected edge density at 1 km. Variance partitioning showed that the four components combined explained 68% of tree aboveground biomass variance (Table Ch2-4), with 32% unexplained. All four variables were significant, however only soils had a pure effect, indicating that in this landscape, soil chemical properties are influencing the variation in tree aboveground biomass.

Discussion

Results from our study indicate that tree AGB, species composition, density, and diversity of seedlings, saplings and trees in secondary forest patches in the San Juan La Selva Biological Corridor respond differently to both landscape spatial configuration and environmental variables, thus confirming our hypothesis. To our knowledge, this is the first study that explicitly combines landscape and environmental variables with patch age to simultaneously assess their effects on composition and structure of recruitment stages in secondary forest patches.

Our soils data values differed from those of Sesnie *et al.* (2009), in which old-growth forest sites were in the same region. Soil texture values in our study were higher in sand content however, values for Ca, pH, Mg and total acidity were lower. This shows that in the SJLS Corridor, soils under secondary forest differ from those of old-growth forests in physical and chemical properties, possibly leading to differences in species composition between the two forest types. Variation in seedling composition was influenced mostly by soils, especially sand, pH, K, Fe, Ca, Mn, P, C and N. Soil carbon recovers faster in secondary forest sites that were former pastures than in former agricultural fields (Weaver *et al.* 1987; Guariguata and Ostertag 2001). Seedling diversity showed a negative relationship with soil sand content, suggesting that the mean value found for this property (52.2%) is probably over the threshold for what is needed to maintain seedling diversity, although more studies are needed to confirm this. We found no relationship between species density and diversity of any recruitment stage with forest age. Usually, species richness and density increase with forest age (Finegan 1996; Chazdon *et al.* 2007). In Puerto Rico, secondary forests on former pastures increased in species richness after 40 years (Aide *et al.* 2000). Variance partitioning for seedling species density suggests dispersal limitation, as it indicated that both climate (isothermality and precipitation of wettest month) and landscape (perimeter to area ratio at 5 km, aggregation index for 1 km and ENN between secondary forests at 500 m) are the strongest factors affecting species density variation. Distance between forest patches and how frequent they are together side by side indicate that landscape spatial configuration is affecting seedling species density more than environmental variables. Variation in seedling diversity could not be assessed because the forward selection process only selected one variable.

Variation in sapling composition did not show any of the variables having a strong influence. The wide range of PCNMs selected, from a finer to a coarser scale, might be the reason for which space explained more the variation in sapling composition, suggesting that it is spatially structured. However, the lack of pure effects of space or any of the other three components indicates that none of them is exerting a greater force over sapling species composition. Tree composition also did not show any sign of either landscape or environmental variables influencing its variation. These results are in accordance with Letcher and Chazdon (2009), who demonstrated that soil properties had little effect on tree composition of species $\geq$ 2.5 cm dbh in secondary forests ranging from 10-42 years of abandonment in the same region. However, variation in soil chemical and physical properties can affect the distribution and structure of secondary forest patches (Guariguata and Ostertag 2001). In the northern area of our study site, Herrera and Finegan (1997) and Finegan and Delgado (2000) have reported floristic heterogeneity of two different types of secondary forest stands dominated by *V. ferruginea* and *Cordia alliodora*. The differences in species diversity, absolute and relative abundances were attributed to differences in topography and soil exchangeable acidity. More studies are required to assess the effects of these specific soil properties on recruitment stages of secondary forests.

Variation in sapling species density was influenced mostly by the landscape. At close distance to the patches at 500 m, the patch area and how frequent the patches appear side by side explained the majority of the variation, along with the clumpiness index at 5 km. With mean patch area, the aggregation and clumpiness indices being important factors in landscape configuration at 500 m and 5 km, it is an indication that the spatial arrangement of secondary forest patches is important in maintaining sapling species density. Variation in sapling diversity was mostly explained by landscape configuration. The shape index remained the strongest component when considering its independent effect (R^2_{adj} = 0.32), suggesting that this measurement of shape complexity is influencing sapling diversity.

Galanes and Thomlinson (2009) found that in secondary forests in Puerto Rico, landscape configuration was positively correlated with composition and richness, and shape, patch size and distance to old-growth forests showed the strongest correlation. Increased distance between old-growth forest fragments have led to differences in species turnover in fragments in the Los Tuxtlas region of Mexico, as different levels of forest cover had greater variation than patch size, slope and altitude (Arroyo-Rodríguez *et al.* 2013). In old-growth forest fragments, landscape configuration has been shown to influence the structure of forest communities, by altering the rate of change for species richness, the demography of trees after disturbance, increasing the mortality of canopy trees, and altering the abundance of pioneer species (Laurance *et al.* 1998; Laurance *et al.* 2000; Benítez-Malvido and Martínez-Ramos 2003). Distance between patches does not seem to be a strong factor affecting forest composition and structure in old-growth forest fragments in Chiapas, Mexico (Hernández-Ruedas *et al.* 2014), as a significant but weak relationship was found between species similarity and distance between sites. Altered microclimatic conditions (Bruna 1999; Benítez-Malvido and Martínez-Ramos 2003) and increased seed predation (Terborgh *et al.* 2001) have reduced seedlings survival and abundance in forest remnants of the Amazon. In African and Amazonian old-growth remnants, seedling abundance and survival have decreased due to reduced animal dispersal (da Silva and Tabarelli 2000; Cordeiro and Howe 2003). Studies have shown that landscape configuration affects richness and composition of secondary forest species (Vleut *et al.* 2015).

Variation in species density in trees shows that the independent effect of soils remained significant after controlling for the effects of the other three components ($R^2_{adj} = 0.15$), indicating that soil chemical properties are controlling for most of the tree species density in these secondary patches. MLM showed that tree diversity was positively related to pH and soil sand content. Soils in our study sites were lower in pH than in the Sesnie *et al.* (2009) study. Soil pH is an important chemical property since it varies inversely with Al toxicity in soils with a pH of 5.3 or lower, and varies directly with base-metal cation availability (Sollins 1998). Variation partitioning indicated that a combination of textural and chemical properties affecting tree diversity in these secondary patches, especially sand, pH and Fe. Sesnie *et al.* (2009) also found that floristic variation for trees ≥ 30 cm dbh and palms ≥ 10 cm dbh in old-growth forests were significantly correlated with sand, clay and soil organic content, with two palm species declining in abundance in sandy-loam soils ≥ 300 m in elevation.

Tree aboveground biomass variation was mostly influenced by soils chemical properties. Variation in biomass in secondary forests is usually related to a change from early-successional species to late-successional species during succession (Brown and Lugo 1990; Rozendaal and Chazdon 2015), however the relative contribution of soils, climate, landscape and space on this variation is not well understood. Usually aboveground biomass increases along succession (Rozendaal and Chazdon 2015), however we did not find any relationship with forest age, probably because our study was not based on chronosequences. Our values for aboveground biomass fluctuated between 47 and 185 Mg, varying in range when compared to values from Rozendaal and Chazdon (2015) in the same study region. Our exclusion of remnant trees from the calculations is an important consideration when assessing AGB is secondary forests, as such trees can add considerable biomass to the plots and alter the true values of a secondary forest stand.

Our study clearly shows the importance of assessing landscape spatial configuration and environmental variables on the composition and structure of recruitment stages. The secondary forests in the Sarapiquí area of our study region have shown resilience when recovering species composition, as mature forest species are recruiting successfully as seedlings, saplings and trees in secondary forest stands, mainly due to the presence of old-growth forest remnants that allow seed dispersal and the presence of generalist species (Norden *et al.* 2009). However, at a landscape scale, we have shown that seedling density and diversity decrease with increasing stand age, and variation in density is influenced by ENN to other secondary forests. We recommend that in order to maintain seedling species density, and overall composition and structure, the current landscape configuration of secondary forest patches in the San Juan La Selva Biological Corridor has to be maintained and an increase in forest cover and closer distances to other secondary forest patches and old-growth fragments are needed. This will allow a continuous movement of seeds from secondary and old-growth forests and assure successful recruitment by sustaining dispersal assemblages (Norden *et al.* 2009). This goal can be achieved by incentivizing landowners to grow more secondary forest on their lands, mainly with Payment for Ecosystem Services and the protection of current old-growth forests.

Further studies are needed to investigate how the landscape along with regional plot soil and climatic data affect both secondary and old-growth forests. We can achieve a more holistic understanding of the factors that affect secondary forest patch composition and structure by incorporating both of these variables as well as regional species pools into future studies of vegetation dynamics and chronosequence (Chazdon *et al.* 2007). Establishing permanent plots to monitor recruitment, mortality and growth rates while incorporating landscape and environmental variables would be very useful for elucidating secondary forest assembly process.

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Tables and Figures

Table Ch2- 1 Summary of soil and climatic properties from 0.25 ha secondary forest patches plots (N=25) in northeastern Costa Rica.

Soil and Climatic Property	**Mean**	**Range**	**SD**
pH	4.23	3.7-4.6	0.19
Acidity (cmol(+)/L)	3.09	1.78-6.01	1
Ca (cmol(+)/L)	0.46	0.09-2.17	0.45
Mg (cmol(+)/L)	0.33	0.12-0.9	0.18
K (cmol(+)/L)	0.08	0.05-0.17	0.03
P (mg/L)	3.87	0.8-10.3	1.99
Cu (mg/L)	9.7	3.5-21	4.1
Zn (mg/L)	1.4	0.3-3.2	0.71
Mn (mg/L)	14	1.8-58.7	15.01
Fe (mg/L)	432.28	152-960	200.32
N (%)	0.34	0.26-0.45	0.05
C (%)	4.21	2.73-5.62	0.71
Sand (%)	52.2	26.6-56.6	12.48
Silt (%)	14.3	7.8-23.6	3.69
Clay (%)	33.5	16.6-57.2	10.55
Elevation (m)	106	0-280	88
Slope (%)	17	2-44	10
Annual Precipitation (mm)	3,925	3,478-4,228	222
Precipitation Seasonality (CV)	30	28-36	3
Min. Monthly Precipitation (mm)	149	105-170	20
Mean Annual Temperature (°C)	26	25.1-26.1	0
Temperature Seasonality (SD x 100)	72	66.9-77.2	3
Min. Temperature Coldest Month (°C)	20	19.7-20.8	0

Table Ch2- 2 Descriptive statistics for aboveground biomass (Mg/ha) for trees ≥ 5 cm dbh in 24 secondary forest plots. Statistics presented are the median, first quartile, third quartile and the minimum and maximum values.

	n	**Median**	**Q1**	**Q3**	**Minimun**	**Maximum**
Aboveground Biomass (Mg/ha)	24	98.1	71.52	135.17	47.89	185.06

Table Ch2- 3 Variation partitioning results for: a) species composition, b) species density, and c) Shannon diversity. Adjusted R² and F statistics presented for all factors, S: soils, C: climate, L: landscape, SP: space. Effects of factors controlling for any combination of other factors denoted by symbol |. Significant relationships are highlighted in bold. N/A (not applicable) indicates analyses that were not performed because no variables were selected by the forward selection. Seedling Shannon diversity was not performed because the forward selection did not select any variables.

a. Species Composition									
	SEEDLINGS			**SAPLINGS**			**TREES**		
Factor	**R^2adj**	**F**	**P**	**R^2adj**	**F**	**P**	**R^2adj**	**F**	**P**
S	**0.24**	**1.83**	**0.0010**	**0.11**	**1.62**	**0.0010**	**0.13**	**1.7**	**0.0010**
C	**0.04**	**2.07**	**0.0010**	**0.07**	**1.93**	**0.0010**	**0.04**	**2.01**	**0.0020**
L	**0.02**	**1.53**	**0.0450**	**0.06**	**1.51**	**0.0010**	**0.08**	**1.5**	**0.0020**
SP	**0.05**	**1.7**	**0.0040**	**0.16**	**1.55**	**0.0010**	**0.11**	**1.76**	**0.0010**
ALL	**0.31**	**1.85**	**0.0010**	**0.25**	**1.45**	**0.0010**	**0.22**	**1.48**	**0.0010**
S | C,L,SP	**0.22**	**1.72**	**0.0010**	0.11	1.31	0.0990	0.06	1.24	0.0800
C | S,L,SP	0.02	1.35	0.1700	-0.05	0.73	0.7760	0.01	1.12	0.3550
L | S,C,SP	0.0010	1.02	0.4240	0.04	1.16	0.3040	0.03	1.15	0.2110
SP | S,C,L	0.02	1.18	0.2270	0.06	1.15	0.1980	0.04	1.18	0.1570

b. Species Density									
	SEEDLINGS			**SAPLINGS**			**TREES**		
Factor	**R^2adj**	**F**	**P**	**R^2adj**	**F**	**P**	**R^2adj**	**F**	**P**
S	0.11	3.87	0.0690	N/A	N/A	N/A	**0.55**	**10.6**	**0.0010**
C	**0.30**	**6.14**	**0.0100**	N/A	N/A	N/A	**0.28**	**5.63**	**0.0080**
L	**0.40**	**6.32**	**0.0030**	**0.49**	**8.59**	**0.0010**	**0.50**	**12.98**	**0.0010**
SP	**0.26**	**5.32**	**0.0150**	**0.24**	**4.76**	**0.0190**	**0.36**	**5.47**	**0.0100**
ALL	**0.73**	**9.15**	**0.0010**	**0.59**	**8.02**	**0.0010**	**0.65**	**5.55**	**0.0030**
S | C,L,SP	0.05	3.88	0.0690	N/A	N/A	N/A	**0.15**	**3.43**	**0.0380**
C | S,L,SP	**0.14**	**5.71**	**0.0130**	N/A	N/A	N/A	-0.01	0.71	0.5030
L | S,C,SP	**0.25**	**6.99**	**0.0040**	**0.36**	**7.42**	**0.0010**	0.02	1.56	0.2500
SP | S,C,L	0.04	2.19	0.1540	**0.11**	**3.77**	**0.0360**	-0.05	0.22	0.9040

c. Shannon Diversity

	SAPLINGS			**TREES**		
Factor	**R^2adj**	**F**	**P**	**R^2adj**	**F**	**P**
S	N/A	N/A	N/A	**0.46**	**7.83**	**0.0040**
C	N/A	N/A	N/A	**0.28**	**10.37**	**0.0080**
L	**0.40**	**16.89**	**0.0050**	**0.24**	**8.5**	**0.0060**
SP	**0.15**	**5.09**	**0.0390**	**0.52**	**9.81**	**0.0010**
ALL	**0.46**	**11.29**	**0.0010**	**0.71**	**8.17**	**0.0020**
S | C,L,SP	N/A	N/A	N/A	**0.11**	**3.36**	**0.0460**
C | S,L,SP	N/A	N/A	N/A	-0.02	0.07	0.7770
L | S,C,SP	**0.32**	**14.50**	**0.0040**	0.05	4.09	0.0640
SP | S,C,L	**0.06**	**3.70**	**0.0640**	**0.16**	**4.49**	**0.0280**

Table Ch2- 4 Variation partitioning results for tree aboveground biomass. Adjusted R² and F statistics presented for all factors, S: soils, C: climate, L: landscape, SP: space. Effects of factors controlling for any combination of other factors denoted by symbol |. Significant relationships are highlighted in bold. N/A (not applicable) indicates analyses that were not performed because no variables were selected by the forward selection.

Aboveground Biomass			
	TREES		
Factor	**R^2adj**	**F**	**P**
S	**0.64**	**21.24**	**0.0010**
C	**0.40**	**8.65**	**0.0020**
L	**0.15**	**5.04**	**0.0330**
SP	**0.43**	**9.56**	**0.0040**
ALL	**0.68**	**7.96**	**0.0010**
S | C,L,SP	**0.21**	**6.86**	**0.0170**
C | S,L,SP	-0.03	0.22	0.8030
L | S,C,SP	0.01	1.55	0.2590
SP | S,C,L	0.01	1.16	0.3490

Figure Ch2- 1 Location of the 25, 0.25 ha plots utilized for the study in the San Juan La Selva Biological Corridor. Sixteen plots were located in Landscape 1, four in landscape 2 and five in Landscape 3

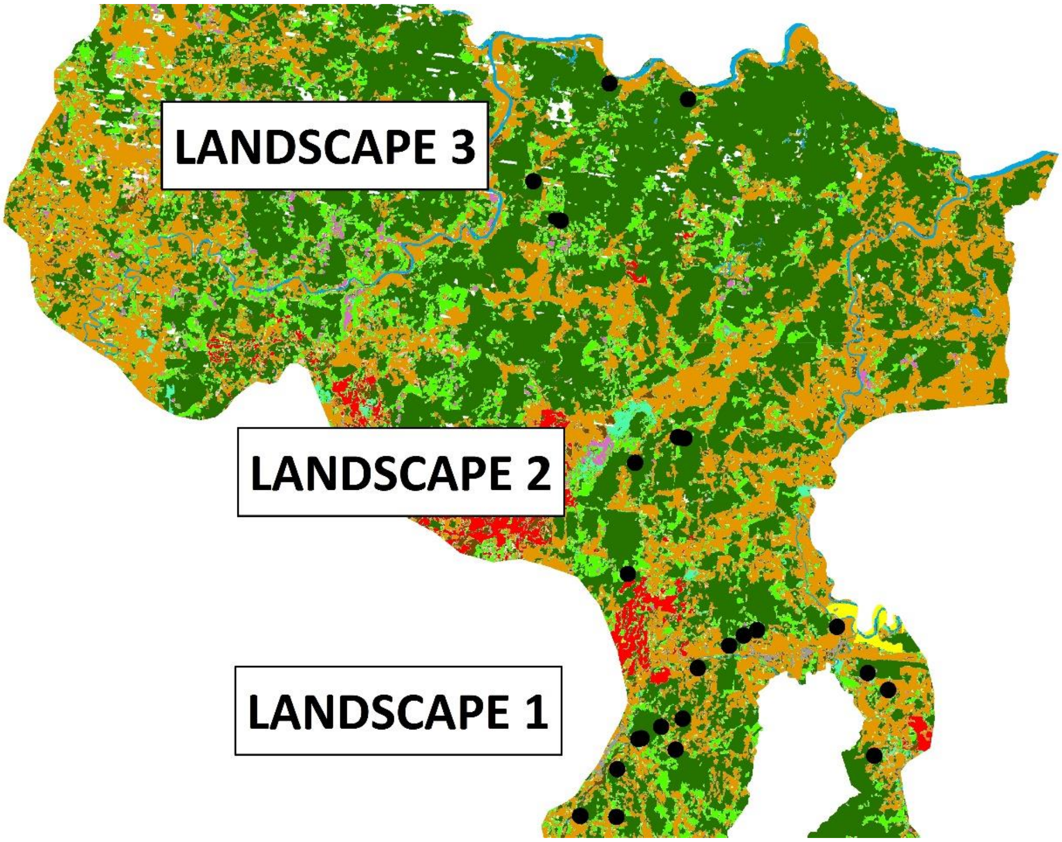
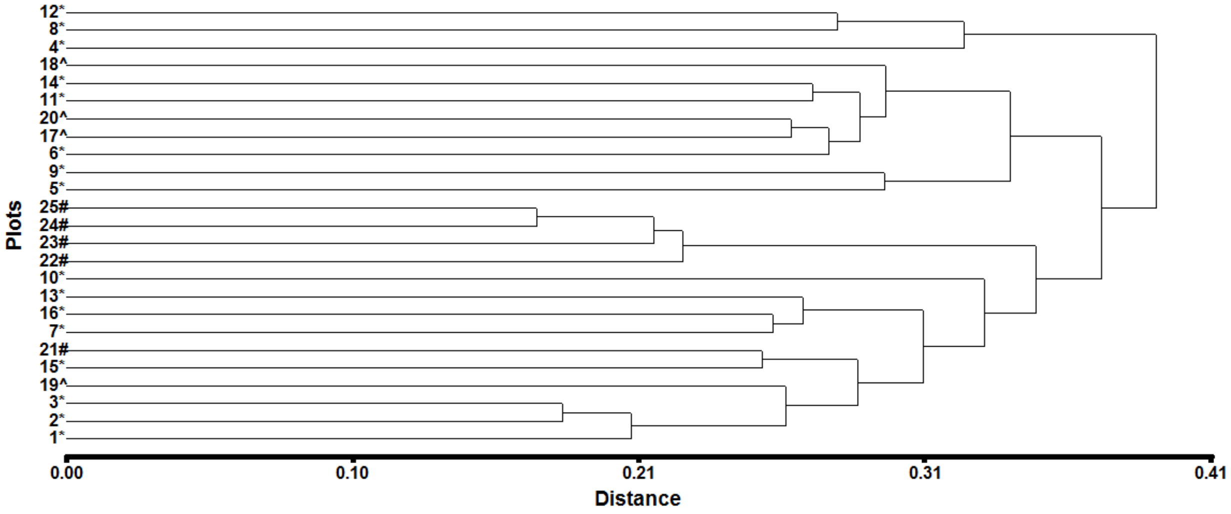
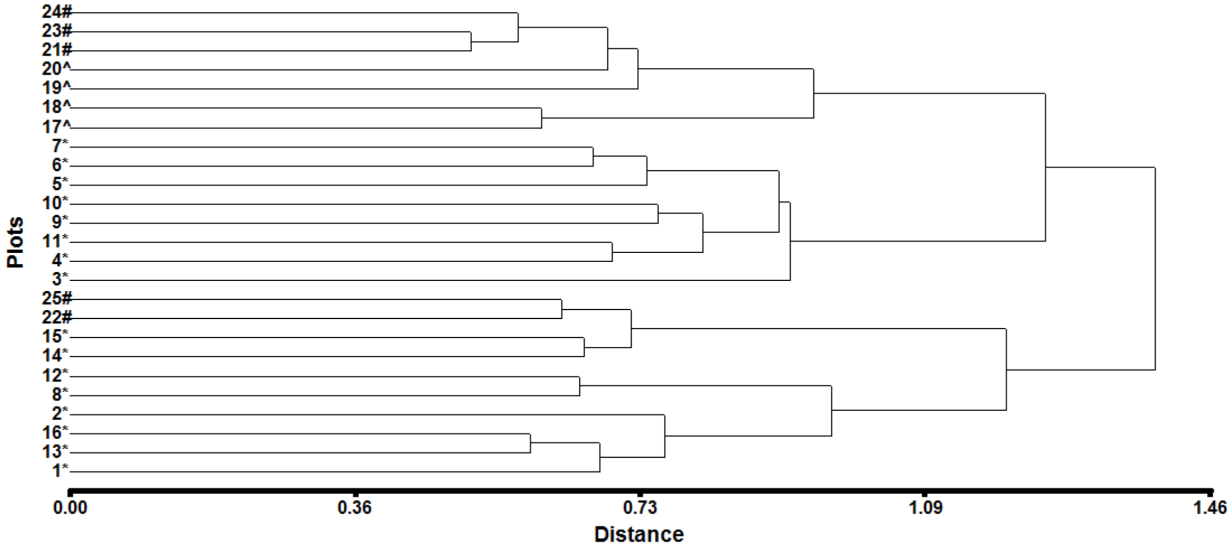


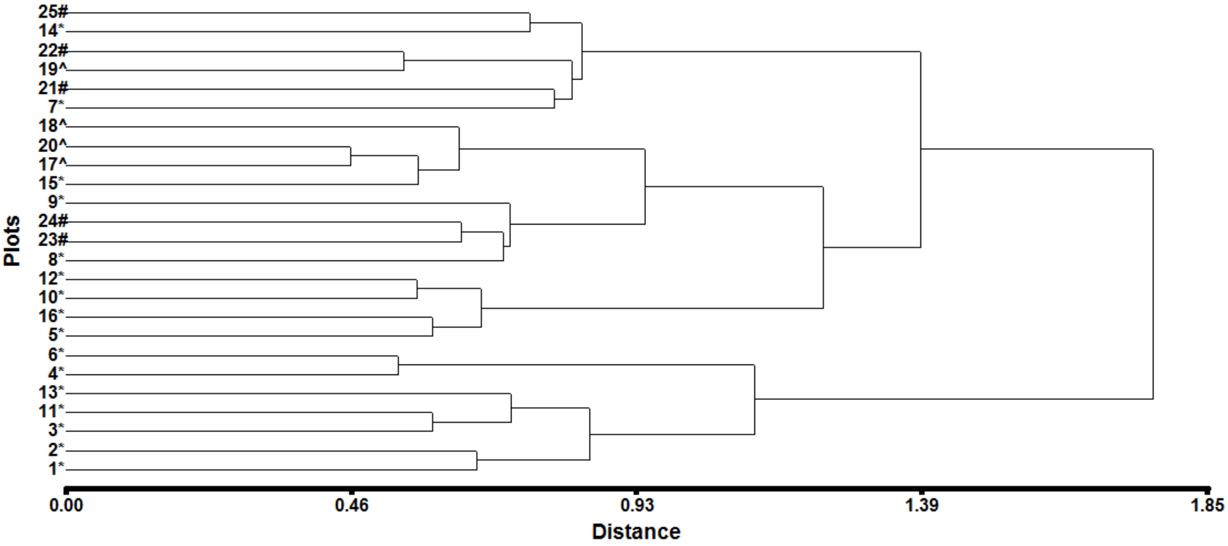
Figure Ch2- 2 Cluster analysis dendrogram (Ward method, Bray-Curtis similarity) for the 25, 0.25 ha secondary forest patches plots in northeastern Costa Rica for: a) seedling composition, b) sapling composition, and c) tree composition. Plots with * symbol are from landscape 1 (1-16), the symbol ^ is from landscape 1 (1-16), the symbol ^ is from plots in landscape 2 (17-20) and plot numbers with the symbol # are from landscape 3 (21-25)



a. Seedling composition

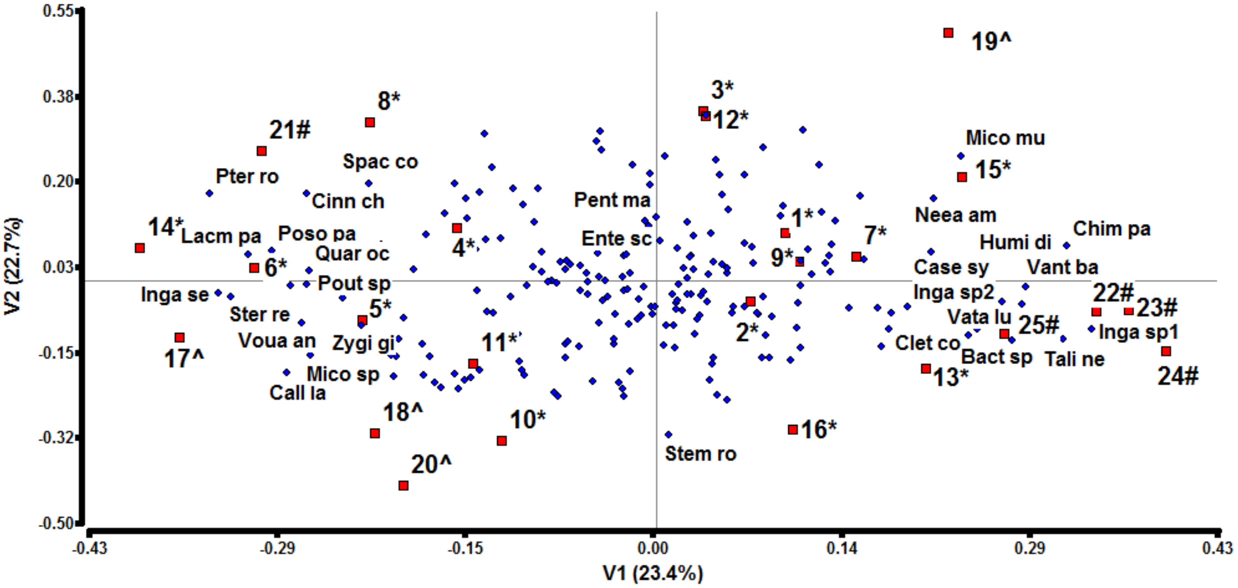


b. Sapling composition

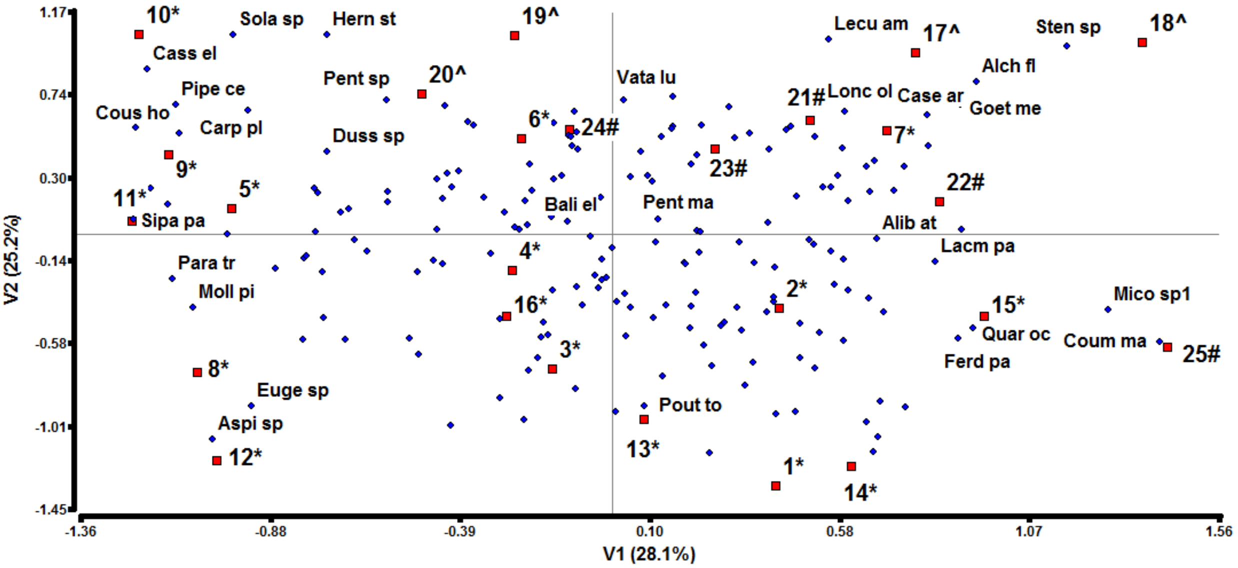


c. Tree composition

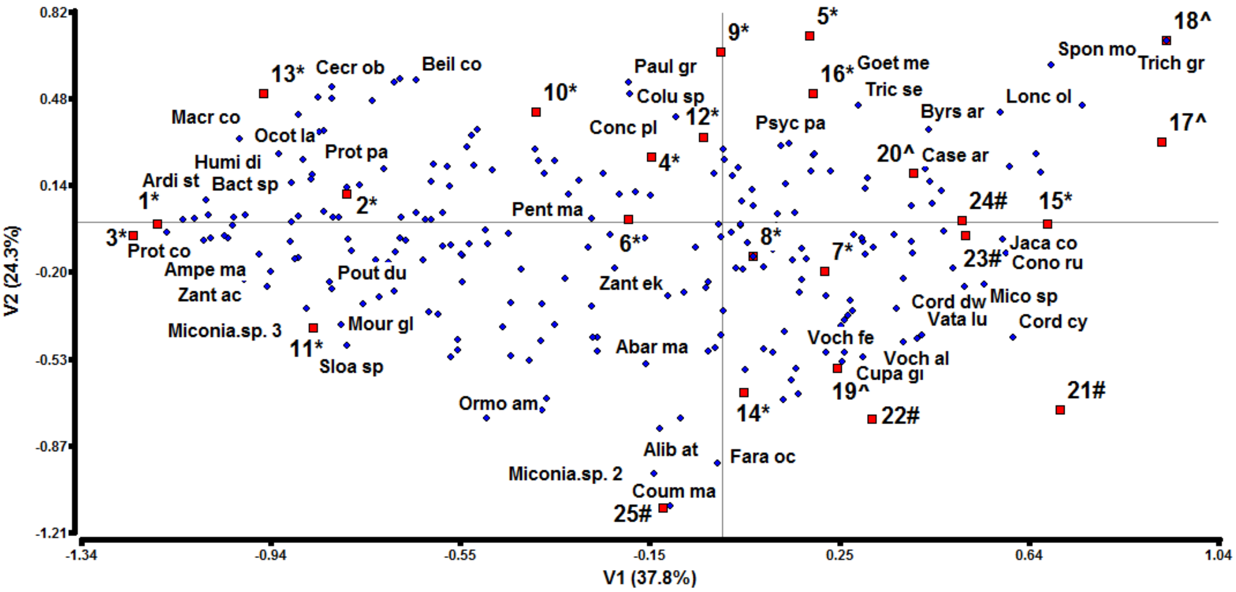
Figure Ch2- 3 Nonmetric Multidimensional Scaling (NMS) ordination of: a) seedling composition, b) sapling composition, and c) tree composition along axis 1 and axis 2 overlaid with the 25 plots. The red squares are plots and the blue diamonds are species. Plots with * symbol are from landscape 1 (1-16), the symbol ^ is from plots in landscape 2 (17-20) and plot numbers with the symbol # are from landscape 3 (21-25). The percent variance explained by each vector is in parenthesis.



a. Seedlings: *Bactris* sp., *Callichlamys latifolia, Casearia sylvestris*, *Chimarrhis parviflora, Cinnamomum chavarrianum, Clethra costaricensis, Enterolobium schomburgkii, Humiriastrum diguense, Inga sertulifera, Inga* sp. 1*, Inga* sp. 2*, Lacmellea panamensis, Miconia multispicata, Miconia* sp.*, Neea amplifolia, Pentaclethra macroloba, Posoqueria panamensis, Pouteria* sp.*, Pterocarpus rohrii, Quararibea ochrocalyx, Spachea correae, Stemmadenia robinsonii, Sterculia recordiana, Talisia nervosa, Vantanea barbourii, Vatairea lundellii, Vouarana anomala, Zygia gigantifoliola*

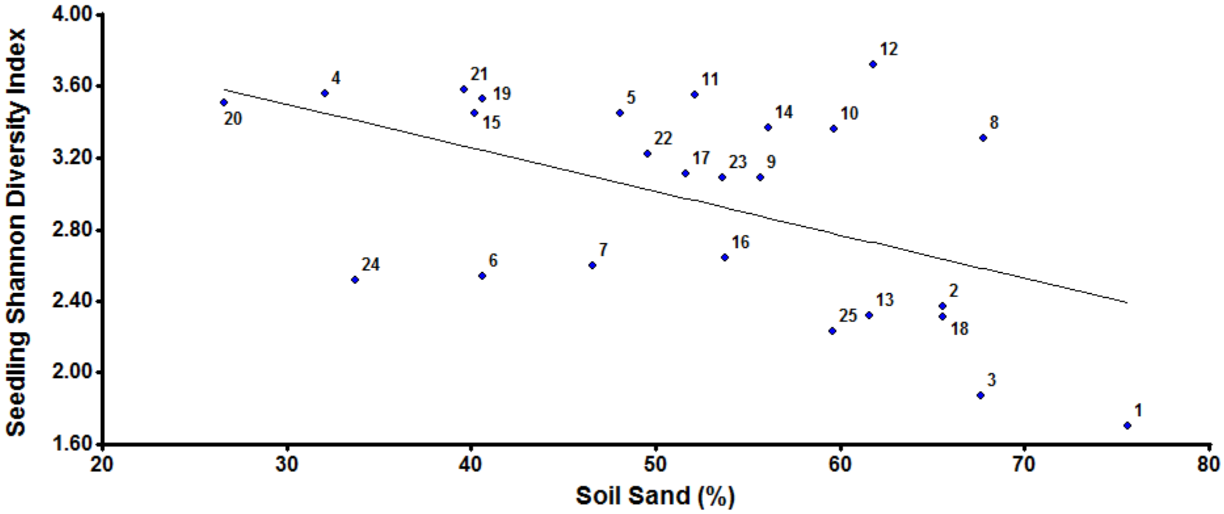


b. Saplings: *Alchornea latifolia, Alibertia atlantica*, *Aspidosperma spruceanum*, *Balizia elegans*, *Carpotroche platyptera*, *Casearia arborea*, *Cassipourea elliptica*, *Couma macrocarpa, Dussia* sp., *Eugenia* sp., *Ferdinandusa panamensis, Goethalsia meiantha, Hernandia stenura, Lacmellea panamensis, Lecuentea amazónica, Lonchocarpus oliganthus, Miconia* sp. 1, *Mollinedia pinchotiana, Parathesis trichogyne, Pentaclethra macroloba, Pentagonia* sp., *Piper cenocladum, Pouteria torta, Quararibea ochrocalyx, Siparuna pauciflora, Solanum* sp., *Stemmadenia* sp., *Vatairea lundellii*



c. Trees: *Abarema macradenia, Alibertia atlantica, Ampelocera macrocarpa, Ardisia standleyana, Bactris* sp., *Beilschmiedia costaricensis, Byrsonima arthropoda, Casearia arborea, Cecropia obtusifolia, Colubrina spinosa, Conceveiba pleiostemona, Conostegia rufescens, Cordia cymosa, Cordia dwyeri, Couma macrocarpa, Cupania glabra, Faramea occidentalis, Goethalsia meiantha, Humiriastrum diguense, Jacaranda copaia, Lonchocarpus oliganthus, Macrolobium costaricense, Miconia* sp., *Miconia* sp. 2, *Miconia* sp. 3, *Mouriri gleasoniana, Ocotea laetevirens, Paullinia granatensis, Pentaclethra macroloba, Pouteria durlandii, Protium confusum, Protium panamense, Psychotria panamensis, Sloanea* sp., *Spondias mombin, Trichilia septrentionalis, Trichospermum grewiifolium, Vatairea lundellii, Vochysia allenii, Vochysia ferruginea, Zanthoxylum acuminatum, Zanthoxylum ekmanni*

Figure Ch2- 4 Negative relationship between seedling Shannon diversity index and soil sand content (R^2= 0.26, P= 0.0088)



Chapter 3: Functional composition and diversity of sapling assemblages in tropical secondary forest patches and their relationship to landscape spatial configuration and environmental variables

Abstract

Tropical secondary forests are an ideal ecosystem to study community assembly. We studied the relative contribution of forest age, soils, climate, landscape configuration and spatial factors influencing sapling assemblages' functional composition and diversity. We sampled six functional traits for 123 species: leaf area, specific leaf area, adult maximum height, leaf dry matter content, leaf nitrogen content and leaf phosphorus content. We found that leaf dry matter content and nitrogen declined with forest age. Community weighted mean variation was mostly influenced by soils, while functional diversity indices were influenced by the plots spatial location. Functional divergence increased with forest age. This study indicates that sapling assemblages' functional composition is influenced by soil physical and chemical properties while functional diversity is highly spatialized and highlights the importance of studying the relative importance of forest age, landscape and environmental variables to better understand community assembly.

Introduction

Tropical secondary forests are patches of natural succession embedded within a matrix of old-growth forest fragments and different agricultural land uses (Norden *et al.* 2009; Shaver *et al.* 2015). These forests, which represent more than half of the world's tropical forest cover (FAO 2010; Rozendaal and Chazdon 2015), are critical not only for biodiversity conservation and ecosystem service provision (Chazdon 2003), but also to our understanding of how plant communities are assembled. Lebrija-Trejos *et al.* (2010) have called secondary forest succession community assembly in action and by studying community functional properties of sapling assemblages in secondary forests, we can gain a better understanding of how plants acquire resources that allow them to be present in these communities. Complex interactions between environmental factors and time of abandonment make it difficult to untangle the relative contribution of each one of these factors influencing species traits values. Adding to this complexity, it has been acknowledged that the spatial context of the surrounding landscape may also impact secondary forest composition and structure (Chazdon *et al.* 2007; Letcher and Chazdon 2009), however the influence of this key factor is surprisingly poorly studied.

The spatial configuration of tropical agricultural landscapes is diverse and complex, with secondary forest patches having a wide range of shapes, areas, edges, distance to other patches and surrounding forest covers (Galanes and Thomlinson 2009; Vleut *et al.* 2015). The high diversity of possible configurations may affect species dispersal, abundance, diversity, structure and richness since the processes that regulate them may be operating at a landscape scale (Turner 1989; McGarigal and McComb 1995; Metzger 2000; Galanes and Thomlinson 2009; Vleut *et al.* 2015). Since secondary forests are naturally patches of vegetation within an agricultural matrix, they are likely to be dispersal limited (Holl *et al.* 2000; Cubiña and Aide 2001; Dalling and Hubbell 2002; Norden *et al.* 2009; Chazdon *et al.* 2010), and this may ultimately have an effect on the community functional traits of the different assemblages, especially in the younger recruitment stages.

Functional traits of tree species, defined as attributes that influence their survival, growth, reproduction and fitness (Ackerly 2003; Poorter *et al.* 2008), are important contributors to our understanding of how species regenerate in secondary forests. Traits of individual species, or functional properties of communities, are related to the age of secondary forests, community assembly and species distribution along environmental gradients (Tilman 1982; Fonseca *et al.* 2000; Keddy 2001; Poorter 2007; Lohbeck *et al.* 2012). One plausible explanation for community assembly is that for a species to be present in a community, it needs to have certain traits that allow it to disperse, establish and recruit under the environmental conditions present in the patch (i.e., overcome dispersal, abiotic and biotic filters) (Lebrija-Trejos *et al.* 2010). This model of environmental control (niche assembly) states that species functional traits relate to the spatial location and environmental conditions present in the patch, and along with the competition to acquire resources, mediates community assembly (Tilman 1982; Norden *et al.* 2009; Sesnie *et al.* 2009). Under this trait convergence scenario, one would expect species with similar trait values to be found in similar habitats. Conversely, under a trait divergence scenario, species with dissimilar trait values will be present in a community because the competition to acquire resources will lead to niche differentiation (Fukami *et al.* 2005; Grime 2006; Pillar *et al.* 2009; Lohbeck *et al.* 2014). Therefore, in the early stages of succession we would expect trait convergence because species need to adapt to the hostile environmental conditions of abandoned pastures; as succession advances we would expect trait divergence and an increase in functional diversity as competition becomes more important (Letcher *et al.* 2012;

Lohbeck *et al.* 2014). In contrast to niche assembly, dispersal assembly states that the actual location of an individual is determined to some extent by the location of the parent (Rosindell *et al.* 2011). When considering the spatial structure of this null model of community assembly, dispersal limitation is parameterized by the relative importance of regional dispersal processes from the surrounding metacommunity compared to the local rates of birth and mortality (Etienne 2007; Rosindell *et al.* 2011). This neutral theory (Hubbell 2001) stipulates that individuals of the same trophic level have the same opportunity of reproduction and mortality irrespective of the species and their abilities to cope with environmental conditions. The neutrality does not assume that all species are equal, it is based on the assumption that demographic rates are stochastic and fitness equivalence is probabilistic (Rosindell *et al.* 2012). Thus, these distance-dependent processes may strongly influence community assembly in secondary forests, more than environmental variables, if secondary forest patches are highly spatially isolated, especially in relation to seed sources (Hubbell 2001; Norden *et al.* 2009; Sesnie *et al.* 2009; Chain-Guadarrama *et al*. 2012; Letcher *et al.* 2012). This is an important consideration when assessing community assembly using functional properties of sapling assemblages, as it is recognized that both dispersal limitation (neutral processes) and environmental variables (niche assembly) influence forest community assembly (Chave 2004; Norden *et al.* 2009; Sesnie *et al.* 2009; Chain-Guadarrama *et al.* 2012). Dissimilar assembly might occur depending on the geographic scale, recruitment stage and along environmental gradients (Cornwell and Ackerly 2009; Mason *et al.* 2013; Lohbeck *et al.* 2014).

Forest age following patch abandonment is also an important predictor of secondary forest community properties. As succession proceeds, species richness, aboveground biomass and basal area tend to increase with stand age (Finegan 1996; Guariguata and Ostertag 2001; Letcher and Chazdon 2009; Lohbeck *et al.* 2012). These changes in forest structure over time occur as the forest canopy closes and shade increases in the understory, as indicated by the model of tropical forest succession (Finegan 1996; Chazdon 2008). This model defines three distinct phases of succession, indicating a possible change in functional trait composition and diversity as early-successional species die out and are replaced by later-successional species. In the first phase, or stand initiation, open fields are characterized by high solar radiation and hostile environmental conditions and are colonized by fast-growing early-successional species. In the second phase, or stem exclusion stage, the canopy starts to close and shade in the understory increases, as the forest structure becomes more complex. During the last phase or understory reinitiation, the canopy is fully closed and the light environment is more heterogeneous (Finegan 1996; Chazdon 2008). Environmental conditions of recently abandoned pastures are hostile and the establishment and recruitment of species is difficult when compared to nearby forests. In abandoned pastures of southern Costa Rica, Holl (1999) found that photon flux density, air temperature and water vapor pressure deficit were greater in the pasture than in the adjacent primary forest. Air temperature was >5°C higher in the pasture than in the forest during the dry season, while soil nutrients and cation-exchange capacity were higher in the forest than in the pastures (Holl 1999). Prior land use intensity could also have an effect on species establishment after abandonment, if the pasture has been burnt repeatedly, exposed to mechanical weeding and overgrazed, then establishment and recruitment will be very slow (Chazdon 2003).

Under this model of forest succession we would expect tree community trait values to range from acquisitive to conservative, as early-successional species, characteristic of early successional high light environments of abandoned pastures, are typically fast growing and have acquisitive traits such as high specific leaf area, large leaves, and high nitrogen foliar content (Poorter and Bongers 2006). As succession proceeds, we would expect to see tree community conservative trait values typical of late-successional slow-growing species that establish under low light environments, such as high leaf dry matter content and wood specific gravity (Reich *et al.* 2003; Garnier *et al.* 2004; Poorter *et al.* 2008; Lohbeck *et al.* 2013; Finegan *et al.* 2015). However, since saplings in secondary forests are established under the canopy and shade is expected to increase during succession, we expect sapling assemblages to increase in leaf area, specific leaf area, leaf nutrient concentration and decrease in leaf dry matter content to achieve more light capturing area and therefore reach the canopy faster. We believe that saplings in secondary forests will have similar community trait values as tree species growing under high light conditions. Similar to this reasoning, Poorter and Werger (1999) hypothesized that adults from understory species have wider crowns, bigger leaf area, and lower leaf area index compared to saplings of similar height. These saplings that are growing towards the canopy developed traits that reduced the biomass per unit height growth, such as slimmer trunks and thinner crowns. Plant strategies to cope with these changes in light and environmental conditions range from acquisitive to conservative and a species position along this continuum is quantified by its functional traits (Wright *et al.* 2004; Lohbeck *et al.* 2013).

Recent research has shown that community assembly can be assessed using the phylogenetic structure of communities if functional traits are conserved within lineages (Chazdon *et al.* 2003; Letcher 2009; Kraft and Ackerly 2010; Letcher *et al.* 2012). Trait convergence occurs because abiotic filtering (environmental factors) exert the strongest influence on community assembly, therefore phylogenetic clustering occurs. Here, functional traits are conserved because closely related species share similar strategies to acquire resources (Webb 2000; Letcher 2009). During the early phases of secondary forest succession, hostile environmental conditions such as high light conditions, temperature and evapotranspiration can adversely affect the establishment of species (Chazdon 2008); those that succeed share similar functional traits that help cope with these conditions. Phylogenetic overdispersion occurs when there is trait divergence; species present in the community will have different values of functional composition and diversity because they are not closely related. Biotic filtering (competition among species) occurs because closely related species will have similar traits and strategies to cope with habitat conditions and could result in competitive exclusion (Webb *et al.* 2002; Letcher 2009; Letcher *et al.* 2012).

Understanding the relative contribution of environmental, landscape configuration, spatial factors and time of abandonment (forest age) regulating the functional properties of sapling assemblages of secondary forest is of critical importance to our knowledge of how community assembly occurs in human-modified landscapes. These factors, or a combination of any of them will influence the traits and eventually dictate what species regenerate in each recruitment stage. Sapling assemblages are an ideal recruitment stage to assess the relative contribution of each of these factors influencing community functional properties. Saplings reflect the effects of dispersal, since the species present in the sapling stage have recruited successfully from the seedling stage, reflect the establishment and recruitment caused by wind and animal dispersed seeds and the seed rain of remnant trees. In this study, our specific objectives were to: 1. quantify functional composition of sapling assemblages; 2. quantify functional diversity using a set of five multidimensional indices; and 3. determine the relative contributions of landscape spatial configuration, environmental variables and stand age as factors affecting the variation in functional composition and diversity of saplings. We hypothesized that under niche assembly theory, species are selected by environmental variables on the basis of their functional traits and the functional properties of sapling assemblages' result from the dependence on autocorrelated environmental variables. Variation in functional composition and diversity among plots is therefore expected to be mainly explained by environmental variables. In contrast, dispersal assembly indicates that species sorting at local communities occurs randomly, but variation in functional composition and diversity are spatially autocorrelated due to spatially limited dispersal. An increase in variation in functional composition and diversity with geographic distances is expected to occur after controlling for the effects of environmental variables. Finally, we hypothesized that as forest age and shade in the understory increases, we expect sapling assemblages community trait values to increase in leaf area, specific leaf area, leaf nutrient concentration and decrease in leaf dry matter.

Methods

Study Area

The study area was located within the San Juan-La Selva Biological Corridor in northeastern Costa Rica, situated mostly between the Sarapiquí and San Carlos counties. It has an area of 245,008 ha, which by 2011 had 58.5% forest cover (47.2% old-growth forest, and 11.3% secondary forests, including native tree plantations) and an agricultural matrix mainly consisting of pasture (32%), and pineapple (2.0%) (Shaver *et al.* 2015). The forests are classified as wet tropical forest in the Holdridge Life Zone (Tosi 1969; Holdridge *et al.* 1975). Plot elevation ranges from 0 to 280 m above sea level (masl). Mean annual precipitation ranges from 3,000 mm in the western lowlands to 4,500 mm in the foothills (Grieve *et al.* 1990; Sesnie *et al.* 2009). The eastern and southern areas of the Corridor receive $\geq$ 150 mm of monthly precipitation throughout the year and the western and northern areas of the Corridor average < 100 mm of rainfall during the driest month (Sesnie *et al.* 2009). Mean annual temperatures average near 24°C in the lowlands (Lieberman *et al.* 1996). The topography of the landscape is characterized by terraces, lowland alluvial flood plains, and low hills (Sesnie *et al.* 2009). Soils are Inceptisols derived from colluvial and alluvial deposits and Ultisols derived from andesitic material. They are very strongly acidic (pH~4) with sandy clay texture of late Tertiary and

Quaternary origin, with development and soil age varying depending on distance from volcanoes, lava flows, and ash falls (Sollins *et al.* 1994).

Study design

We established 25, 0.25 ha (50 × 50 m) plots across the study area. The study area was divided into three landscapes, with 16 plots in Landscape 1, 4 in Landscape 2 and 5 in Landscape 3. Each landscape has different surrounding forest covers and soil properties. Twenty-one plots were established in former pastures and 4 in areas that were cleared but not used. Forest ages ranged between 15-54 years post-abandonment. Santiago-García *et al.* (Chapter 2) measured diameter at breast height (dbh-1.3m) and identified every stem between 1-4.9 cm, defined here as saplings (Norden *et al.* 2009) in three 50 × 5 m transects per plot. Sapling transects were separated by 20 m. We also measured and identified every stem $\geq$ 5 cm dbh for each individual tree species.

We selected traits for sampling considered important for plant performance that reflect different ecological strategies and are known to vary across environmental gradients (Cornelissen *et al.* 2003; Wright *et al.* 2004; Ackerly and Cornwell 2007; Chave *et al.* 2009; Cornwell and Ackerly 2009; Laliberté *et al.* 2010; Lohbeck *et al.* 2012), namely: leaf area (mm^2), specific leaf area ($cm^2 g^{-1}$), leaf dry matter content ($mg\ g^{-1}$), leaf nitrogen content (N mass, in %), leaf phosphorus content (P mass, in %) and adult maximum height (m). We calculated basal area for saplings in each plot, and selected species for sampling that accounted for 80% of the total sapling basal area value, representing the dominant species of each plot. This approach is based on the assumption that dominant species have a greater influence on ecosystem process than rare species, and also best represent community or assemblage response to environmental factors (Grime 1998; Lohbeck *et al.* 2012; Finegan *et al.* 2015).

Functional traits sampling followed methods based on Garnier *et al.* (2001) and Cornelissen *et al.* (2003), but adjusted for saplings. Collection was performed avoiding atypical sites (steep hills, flooded areas) and we selected shaded, totally expanded young leaves, that presented no signs of herbivory or disease, to the extent possible. To sample leaf area, specific leaf area and leaf dry matter content, we collected five leaves per individual and five individuals per species. If the species fell within the 80% total plot basal area value in more than one landscape, it was collected in the respective landscape, for a maximum of 15 individuals per species if it was collected in the three landscapes. In total, we sampled functional traits of saplings of 123 woody species. Of these, 47 were collected and measured once, 44 were collected and measured twice and 32 species were collected in the three landscapes. After field collection, samples were rehydrated in the laboratory for at least six hours. Once the leaves were rehydrated, excess water was removed and leaves were immediately weighted to obtain fresh weight. Whole simple leaves or whole leaflets for compound leaves (without the petiole or raquis) were scanned in black and white with the Leaf Area Measurement software (University of Sheffield, U.K.) with a 600 dpi resolution. Big leaves were divided in sections and later added up. After scanning, leaves were oven-dried at 65°C for 48 hours and immediately weighted to obtain dry weight. The whole sample was weighted and the total weight divided by the number of leaves. The mean leaf dry matter content (LDMC) was obtained by dividing the fresh weight of each leaf by its dry weight and averaging the five values to obtain an average by individual. For specific leaf area (SLA), the average was calculated by dividing the area of each leaf by its dry weight and averaging the five values to obtain an average by individual. To analyze nitrogen and phosphorus foliar content, a homogeneous sample per species was obtained from the five individuals collected. Samples were handled as described above, except that samples did not require rehydration. Samples were analyzed at the Soils Laboratory of the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE-Turrialba, Costa Rica). Adult maximum height (Hmax) was obtained from an existing database for the tree species of the study area (see Finegan *et al*. 2015) (64 species) and the flora of the La Selva Biological Station (59 species).

For each plot, we located its center after delimiting the perimeter using a Garmin GPS 60csx (Garmin International, Olathe, KC, US-accuracy of ± 3 m). Around each plot center, we calculated 15 landscape variables within a 500 m, 1 km and 5 km radius using the 2011 land use map developed by Shaver *et al.* (2015). The metrics quantified the total area of secondary forest, percent forest cover of secondary forest, percent forest cover of mature forest, number of patches, patch density, largest patch index, total edge, edge density, mean patch area, patch shape index, perimeter to area ratio, Euclidean Nearest Neighbor (ENN) between secondary patches, ENN between secondary forest patches and mature forests, and clumpiness index. Metrics were calculated with Fragstats 4.2 (McGarigal *et al.* 2012). We obtained 19 bioclimatic variables from WorldClim (http://www.worldclim.org). This is a bioclimatic data set with 30 arc-second grids and 1 km^2 spatial resolution. To evaluate soil physical and chemical properties, we collected 5 samples in each plot at 40 cm depth, one in each corner and one at the plot center, with organic material cleared from the first 2 cm prior to auguring (Sesnie *et al.* 2009). We placed the samples in labeled plastic bags and air-dried them prior to analysis. The Soils Laboratory at CATIE analyzed the soil samples for each plot for pH, extractable K, P, Ca, Cu, Zn, Mn, Fe, Mg, percent N, percent C, and total acidity (indicator of potential aluminum toxicity). Cu, Zn, Mn, Fe, K and P extractions were measured using Modified Olsen extraction at a pH of 8.5. Total acidity, Ca, and Mg extractions were done using potassium chloride (KCl), soil pH in water and N and C by combustion in an autoanalyzing equipment. Soil texture characteristics (% sand, silt and clay) were determined using the Bouyoucos method and textural classes were assigned following USDA Soil survey standards.

Data analysis

Functional composition was assessed as community weighted means (CWM) and represented as a table of abundance-weighted mean trait values per plot per landscape (Violle *et al.* 2007). For each plot, we combined the data from the three transects to make one sample. This measurement represents the expected value of a trait of an individual randomly selected from the community and its mean is calculated based on a representative value for each species and its relative abundance (Garnier *et al.* 2004; Díaz *et al.* 2007; Lavorel *et al.* 2007; Casanoves *et al.* 2011). Functional diversity (FD), defined as the value, range, distribution and relative abundance of the functional traits of a particular organism in an ecosystem (Díaz *et al.* 2007), was assessed using a set of complimentary multi-trait and multidimensional indices that have been proposed to jointly assess the functional characterization of a community (Villéger *et al.* 2008; Laliberté and Legendre 2010). These explore the different aspects of functional diversity: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), and functional dispersion (FDis). Functional richness represents the volume occupied by the community in the multivariate trait space by identifying the species with extreme trait values and then estimating the volume of the community in the trait space. Functional evenness, independent of FRic, measures the regularity by which species are distributed in the trait space using its abundance. This index, which requires at least three species in each sample, varies between zero and one, with zero being a lack of equity and one complete equity or evenness. The value of the index decreases when the distribution of the species abundance is less uniform. Functional divergence quantifies the scattering of trait values in the multivariate space by showing how species abundances are distributed in the trait space. Functional dispersion is the average distance of each species to the centroid of the community of trait space. Species abundances are used to calculate the weighted centroid (Villéger *et al.* 2008; Laliberté and Legendre 2010; Casanoves *et al.* 2011). These analyses were performed using FDiversity software (Casanoves *et al.* 2011, www.FDiversity.nucleodiversus.org).

To detect relationships between forest age and CWM's and functional diversity indices, we performed mixed linear mixed models (MLMs) since the residuals had a normal distribution. To test for normality, we performed Shapiro-Wilks test. MLMs allow the use of planar coordinates of the study plots (CRTM05) as co-variables to address the issue of lack of spatial independence. To quantify the amount of variance explained by soils, climate, landscape spatial configuration and spatial variables we performed a variation partitioning analysis (Borcard *et al.* 1992; Legendre 2008) on functional composition and functional diversity. For functional composition, the response matrix was the CWM of trait values and for functional diversity, the response matrices were the four complementary indices. A separate analysis was done for each one. The predictor variables were soil physical and chemical properties, landscape metrics, climatic variables and the spatial component represented by a set of positive eigenvector values generated from a geographic Euclidean matrix of plot coordinates using a principal coordinates of neighbor matrices (PCNM) analysis (Borcard and Legendre 2002).

Results

Descriptive statistics of community weighted means and functional diversity indices are shown in Table Ch3-1. Principal Components Analysis (Figure Ch3-1) shows the spectrum of plot functional composition in CWM trait space, with axis 1 explaining 43.7% of the variance, and axis 2 explaining 32.6% of the variance. Three plots from landscape 1 and one plot from landscape 2 are at the end of high N and SLA spectrum, possibly indicating that these plots share these characteristics of early-successional forests, however these four plots range from 32 to 38 years old. High LDMC appears on the gradient as high SLA and high N (Table Ch3-2), which appears contradictory to the usual findings on early-successional forests where there are thin, nutrient-rich leaves with high SLA. All plots from landscape 3 appear to show low LDMC, N and SLA. Higher CWM of Hmax were present on three plots from landscape 1, one from landscape 2 and all five from landscape 3. CWM leaf area showed no particular plot associated towards the high end of the spectrum, nevertheless at the lower end there were three plots from landscape 1 and one from landscape three, indicating that these plots have the lowest CWM of leaf area.

Relationship between forest age and functional properties of sapling assemblages

We found no relationship between FEve, FRic, FDis and forest age. FRic presented problems with the variance, preventing it from finding any relationship with forest age. We observed a positive relationship between Functional Divergence and forest age (R^2= 0.55, P= 0.0001) indicating that as age of abandonment advances, the dispersion of the trait values in the multivariate space increases (Figure Ch3-2). This index reflects the distribution of species abundances in the trait space. We found no relationship between leaf area, specific leaf area, foliar P and adult maximum height with forest age. There was a weak negative relationship between forest age and leaf dry matter content (Figure Ch3-3) (R^2= 0.26, P= 0.0103). This indicates that as succession advances, LDMC decreases in sapling assemblages, thus ranging from conservative to acquisitive. We also found a negative relationship between CWM leaf nitrogen content and forest age (R^2= 0.28, P= 0.0070) (Figure Ch3-4). This result indicates that as succession advances, sapling assemblages' nitrogen content decreases, ranging from higher content (acquisitive) to lower content (conservative). We found no relationship between any of the functional indices and tree basal area, suggesting that this ecosystem property is not affected by the functional diversity of sapling assemblages.

Variance Partitioning

Community Weighted Mean (CWM)

The forward selection procedure retained two principal coordinates of neighbor matrices (PCNMs) for modeling functional composition, PCNM 2 and PCNM 13. The final soil components related to the overall variation in CWMs included Cu, pH and silt, the climate components retained were precipitation of warmest quarter and precipitation of coldest quarter and the landscape component was the Shape Index at 5 km. The variance partitioning showed that soils, climate, landscape and space explained 45% of the overall variation in functional composition while 55% remained unexplained (Table Ch3-3). Soils explained more the variation in CWM in comparison with climate, landscape and space. These results are further confirmed when observing the significant pure effects of soils when controlling for the effects of the other three variables, indicating that the combination of soil chemical and physical properties is influencing the variation in CWM. The landscape component was also significant when controlling for the other three variables, indicating that the Shape Index, which measures the complexity of patch size compared to a standard shape (square) of the same size, is influencing CWM variation.

Functional Diversity Indices

The forward selection procedure for the four functional diversity indices is shown in Table Ch3-4. We found no evidence of influence of climate on functional diversity as no climatic variables were chosen for any of the four functional diversity indices. For functional richness, soils, landscape and space explained 66% of the variation, while 34% remained unexplained (Table Ch3-5). The spatial factor explained the greatest variation, and it remained the strongest factor when controlling the other two, indicating that sapling functional richness is spatialized at intermediate-to-fine scales. For functional evenness, soils, landscape and space, explained 96% of the observed variation, and 4% remained unexplained (Table Ch3-5). The spatial variable was the strongest factor and remained the strongest when controlling for soils and landscape, again indicating that sapling functional diversity, as measured by functional evenness, is highly spatialized. For FDiv, all variables explained 43% of functional divergence variation, while 57% remained unexplained (Table Ch3-5). The landscape configuration was the strongest and this was confirmed when controlling for soils and the spatial variables, indicating that the shape index at 1 km radii and mean patch area of secondary forests at 5 km radii are influencing the variation in functional divergence. For FDis, spatial, soils and landscape variables explained 81% of sapling functional dispersion, while 19% remained unexplained (Table Ch3-5). Spatial variables were the strongest and remained the strongest when controlling for soils and landscape, indicating sapling functional dispersion is spatialized at intermediate and coarse scales. The shape index at 1 km also influenced FDis variation, albeit not that strongly when compared to the PCNMs.

Discussion

In this study we asked how the relative importance of landscape spatial configuration, environmental variables and stand age influenced the functional composition and diversity of sapling assemblages in secondary forest patches. We found that the variation in functional composition, measured as the community-weighted means of six functional traits, was influenced mostly by soil chemical and physical properties, especially Cu, pH and silt content. Soils in the study plots were very strongly acidic, with a mean pH of 4.23, Cu varied greatly among plots (3.5-21 mg/L) and silt had the lowest mean values and standard deviation (14.3% and 3, respectively) compared to sand and clay content. There was limited variability in the CWM values for the six functional traits measured, except for leaf area (S.E. 931.1) and to a lesser extent LDMC (S.E. 8.68). The great variability in leaf area might be due to the large number of species sampled (n= 123) and the consequent effects of having varying leaf areas from different species and repeated measures from different landscapes. Our CWM values for specific leaf area were higher, and leaf dry matter content and adult maximum height were lower than those found by Finegan *et al.* (2015). The values from Finegan *et al.* (2015) were based on individuals' ≥10 cm dbh on primary forest plots from Costa Rica, Brazil and Bolivia (the Costa Rica site is located near our study region). The differences in trait values are most likely due to the differences between mature and secondary forest plots, the climatic and edaphic differences between the sites and distinct recruitment stages (saplings and trees). The difference in values could also be due to the trait values found in Finegan *et al.* (2015) were from canopy trees while our values were from saplings growing under the shade, which might explain why our CWM values for SLA were higher, and leaf dry matter content and adult maximum height were lower. Sapling assemblages might have higher SLA and lower LDMC values (resulting in more surface area and softer leaves) as it allows them to capture more light in the forest understory to fuel growth to reach the canopy. Hmax could be lower because the species composition of the sapling assemblages in our study was different from the Finegan *et al.* (2015) study which included canopy tree species.

Soil nutrient availability is part of the reason for which there exist a spectrum of variability in leaf traits; habitats with low nutrient contents and low productivity are usually associated with conservative traits, and habitats with high soil nutrient contents and high productivity are associated with acquisitive traits (Wright and Westoby 2003; Lohbeck *et al.* 2013; Finegan *et al.* 2015). Generally, soils with low N and P have tree species with low SLA, leaf N and leaf P (Meziane and Shipley 2001; Paoli 2006; Ordoñez *et al.* 2009), however this trend might not apply to sapling assemblages. Finegan *et al.* (2015) found that CWM and Hmax of trees were positively related to biomass increments and these increments were negatively related to CWM of wood specific gravity, indicating that stands that have higher productivity are characterized by tree species communities with soft wood and soft and short-lived leaves. Moreover, they found that forest stands with high values of CWM SLA and foliar P have higher biomass production. Using a global dataset of ten countries including a range of ecosystems, from tundra to tropical forests, Ordoñez *et al.* (2009) found that SLA and leaf nitrogen content were positively related to soil total P and N mineralization and negatively to C:N ratio, with foliar P being positively related to soil P availability and to mean annual temperature, mean annual precipitation, potential evapotranspiration and irradiance. Overall, they found that the variation in individual leaf traits responded more to soil nutrients than to climate (Ordoñez *et al.* 2009). Studies at global and local scales have demonstrated the link between soil fertility and leaf traits, but also showed that not only soils but climatic factors can also regulate leaf traits (Wright *et al.* 2005; Ordoñez *et al.* 2009). It has been shown that across climatic gradients, mean values of certain traits can vary (Wright *et al.* 2005; Ackerly and Cornwell 2007). However, in our study neither functional composition nor diversity of saplings were related to climatic variables.

Leaf dry matter content had a negative relationship with forest age, declining as age of abandonment increased, thus confirming our hypothesis that LDMC would decrease as succession proceeds. Usually, high values of this conservative trait are found in latter successional forests (Kitajima and Poorter 2010; Finegan *et al.* 2015). Lohbeck *et al.* (2013) found that LDMC increased with stand basal area in wet forests of Mexico. Sapling assemblages with thin leaves might be a response to being in the shade and not being able to photosynthesize enough to store nutrients; however it has been found that tree species in the forest understory or on weathered soils usually have thick, tough leaves with long lifespan. The lifespan of a leaf and the age of a sapling can vary widely, as it has been found that saplings of 1 cm dbh can have a median age of 17 years (Hubbell 1998) and generalizing about leaf and sapling age for so many species is difficult. We also observed a negative relationship between sapling community foliar N and forest age, with N declining as forest age increases. We hypothesized the opposite trend, however this follows the expected acquisitive-conservative continuum of traits characteristic of early successional communities changing to more conservative traits as succession proceeds (Poorter *et al.* 2004).

There was no relationship between forest age and three functional diversity indices. This result agrees with Lohbeck *et al.* (2012) in which they found no relationship between functional diversity and time of abandonment in secondary forests in Mexico. However, we observed an increase in functional divergence as forest age increased, indicating that probably the distribution of species abundance in the trait space increases in older plots. Also, in contrast with the findings of Lohbeck *et al.* (2012), we did not observe any relationship between functional diversity and tree basal area. The variation in three of the functional diversity indices (FRic, FEve and FDis) was mostly explained by spatial variables or the actual geographical location represented by the PCNM's. Surprisingly, neither soil nor climatic variables explained the variability in these functional diversity indices when controlling for the other factors, indicating that sapling functional diversity is highly spatialized. Variation in functional divergence was mostly explained by landscape factors, specifically mean patch area at 5 km and shape index at 1 km. This index measures the dispersion of the trait values in the multivariate trait space and also reflects the distribution of species abundance in the trait space (Casanoves *et al.* 2011). Greater mean patch area and a complex patch geometry may be needed to maintain the variation in functional divergence of saplings. It is important to note that functional richness might not be the optimal index to represent the traits hypervolume in a community since it is highly correlated to species richness (Villéger *et al.* 2008; Finegan *et al.* 2015). An alternate index may be more suitable to measure the volume occupied by the trait space, such the Convex Hull (Cornwell *et al.* 2006). Additionally, in our study, it presented problems with its variance and the distribution of residuals.

In conclusion, sapling assemblages' variation in functional composition in secondary forests was influenced mostly by soil chemical and physical properties, while functional diversity was largely dictated by the geographical location of the plots. Landscape spatial configuration only had an effect in the variation of functional divergence, but not in the other functional diversity indices or functional composition. Forest age had an opposite effect on the CWM values of LDMC, thus highlighting the importance of making the distinction of what is expected in terms of trends in community trait values in saplings and trees. To our knowledge, this is one of the first studies that explains the variability in functional composition and functional diversity in saplings of tropical secondary forest patches considering the effects of landscape spatial configuration, environmental variables and forest age. There is a paucity of information regarding sapling functional traits in tropical secondary forests and more research is needed where mechanistic explanations are sought to explain the variation in functional composition and diversity. It is also important to differentiate between recruitment stages, as it is not expected that the same factors that influence or regulate functional composition and diversity of tree communities would operate in sapling or seedling communities.

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Tables and Figures

Table Ch3- 1 Descriptive statistics for functional properties of sapling assemblages in secondary forests in 25 plots of 0.25 ha. Table shows functional composition (Community Weighted Means) for leaf area, specific leaf area (SLA), leaf dry matter content (LDMC), phosphorus content (P), nitrogen content (N) and adult maximum height (HMax) and functional diversity indices: Functional Richness (FRic), Functional Evenness (FEve), Functional Divergence (FDiv) and Functional Dispersion (FDis).

Variable	Mean	Standard Error	Minimum	Maximum
CWM Leaf Area (mm2)	17,225.48	931.1	6,066.82	23,021.59
CWM Specific Leaf Area (cm2 mg -1)	18.73	0.44	15.06	22.58
CWM Leaf Dry Matter Content (mg g -1)	298.45	8.68	194.56	418.88
CWM Leaf Nitrogen Content (%)	2.48	0.06	1.82	2.96
CWM Leaf Phosphorus Content (%)	0.11	0	0.07	0.15
CWM Maximum Potential Height (m)	22.91	1.07	10.94	32.03
Functional Richness	6.97	2.03	0.01	45.38
Functional Evenness	0.67	0.02	0.48	0.84
Functional Divergence	0.77	0.02	0.6	0.96
Functional Dispersion	1.77	0.08	1.15	3

Table Ch3- 2 Eigenvectors for the Principal Components Analysis of Community-Weighted Means (CWM) trait values of sapling assemblages.

Variables	**e1**	**e2**
CWM Leaf Area	0.06	0.21
CWM SLA	0.63	-0.18
CWM LDMC	0.4	0.39
CWM P	-0.08	0.63
CWM N	0.62	0.21
CWM Hmax	-0.24	0.57

Table Ch3- 3 Variation partitioning results for Community Weighted Means. Degrees of freedom, adjusted R², F and P statistics presented for all factors, S: soils, C: climate, L: landscape, SP: space. Effects of factors controlling for any combination of other factors denoted by symbol |. Significant relationships are highlighted in bold.

	Community Weighted Means			
Factor	**Df**	**R^2adj**	**F**	**P**
S	**3**	**0.28**	**4.05**	**0.0010**
C	**2**	**0.23**	**4.66**	**0.0020**
L	**2**	**0.11**	**2.47**	**0.0330**
SP	**2**	**0.18**	**3.57**	**0.0020**
ALL	**9**	**0.45**	**3.23**	**0.0010**
S | C,L,SP	**3**	**0.10**	**2.06**	**0.0330**
C | S,L,SP	2	0.06	1.86	0.0990
L | S,C,SP	**2**	**0.07**	**2.16**	**0.0290**
SP | S,C,L	2	0.01	1.11	0.3700

Table Ch3- 4 Soil, climate, landscape and spatial (PCNM's) variables selected by the forward selection procedure for the Functional Diversity Indices of sapling assemblages: Functional Richness, Functional Evenness, Functional Divergence and Functional Dispersion. Soils and landscape variables are C: % carbon, Cu: copper, K: potassium, MPA: mean patch area of secondary forests and Shape Index (measures the complexity of patch size compared to a standard shape (square) of the same size).

Variable	**Functional Richness**	**Functional Evenness**	**Functional Divergence**	**Functional Dispersion**
Soils	C, Cu	K	pH	C
Climate	None	None	None	None
Landscape	% secondary forest 1 km	Shape Index 1 km	Shape Index 1 km, MPA 5 km	Shape Index 1 km
Space (PCNM)	9, 10, 20, 21	1, 2, 4, 6, 11, 13, 14, 16, 17, 18, 22, 23	10	9, 10, 11, 13, 19, 20, 21

Table Ch3- 5 Variation partitioning results for Functional Diversity Indices: Functional Richness, Functional Evenness, Functional Divergence and Functional Dispersion of sapling assemblages. Degrees of freedom, adjusted R^2, F and P statistics presented for all factors, S: soils, L: landscape, SP: space. Effects of factors controlling for any combination of other factors denoted by symbol |. Significant relationships are highlighted in bold.

	Functional Richness				**Functional Evenness**				**Functional Divergence**				**Functional Dispersion**			
Factor	**Df**	**R^2adj**	**F**	**P**	**Df**	**R^2adj**	**F**	**P**	**Df**	**R^2adj**	**F**	**P**	**Df**	**R^2adj**	**F**	**P**
S	**2**	**0.37**	**8.2**	**0.0010**	**1**	**0.15**	**5.25**	**0.0220**	**1**	**0.14**	**4.93**	**0.0370**	**1**	**0.22**	**7.61**	**0.0100**
L	**1**	**0.35**	**13.89**	**0.0030**	**1**	**0.14**	**5.04**	**0.0310**	**2**	**0.24**	**4.80**	**0.0310**	**1**	**0.15**	**5.31**	**0.0380**
SP	**4**	**0.56**	**8.76**	**0.0020**	**12**	**0.97**	**59.76**	**0.0010**	1	0.11	4.09	0.0600	**7**	**0.76**	**11.65**	**0.0010**
ALL	**7**	**0.66**	**7.56**	**0.0010**	**14**	**0.96**	**43.90**	**0.0010**	**4**	**0.43**	**5.57**	**0.0040**	**9**	**0.81**	**12.52**	**0.0010**
S | L,SP	2	0.01	1.35	0.2710	1	-3.50E-03	4.40E-03	0.9460	1	0.05	2.82	0.1070	1	-0.01	0.40	0.5450
L | S,SP	1	0.06	4.26	0.0600	1	-2.50E-03	0.28	0.6030	**2**	**0.24**	**5.62**	**0.0070**	**1**	**0.05**	**5.22**	**0.0490**
SP | S,L	**4**	**0.18**	**3.72**	**0.0240**	**12**	**0.71**	**35.09**	**0.0010**	1	0.09	4.25	0.0640	**7**	**0.54**	**10.03**	**0.0010**

Figure Ch3- 1 Principal Components Analysis of Community Weighted Means trait values for the 25 secondary forest patches plots. Plots are represented by blue circles and trait values are yellow circles. Plots with * symbol are from landscape 1 (1-16), the symbol ^ is from plots in landscape 2 (17-20) and plot numbers with the symbol # are from landscape 3 (21-25).

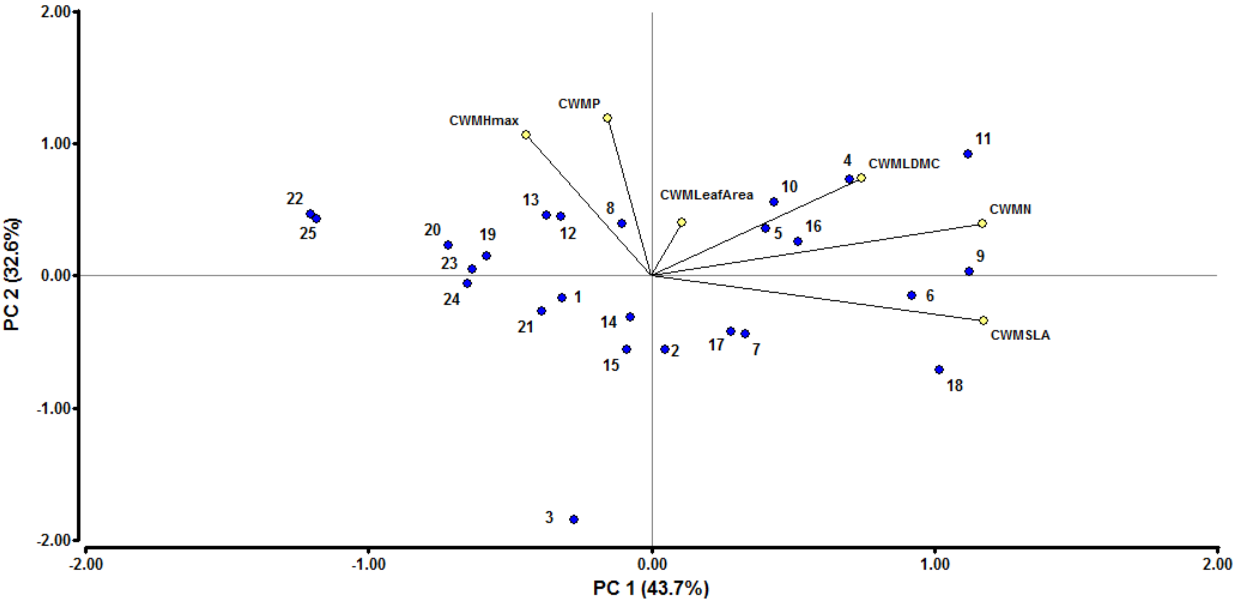


Figure Ch3- 2 Relationship between forest age and Functional Divergence (R^2= 0.55, P= 0.0001) of saplings along 24 0.25 ha plots of secondary forest.

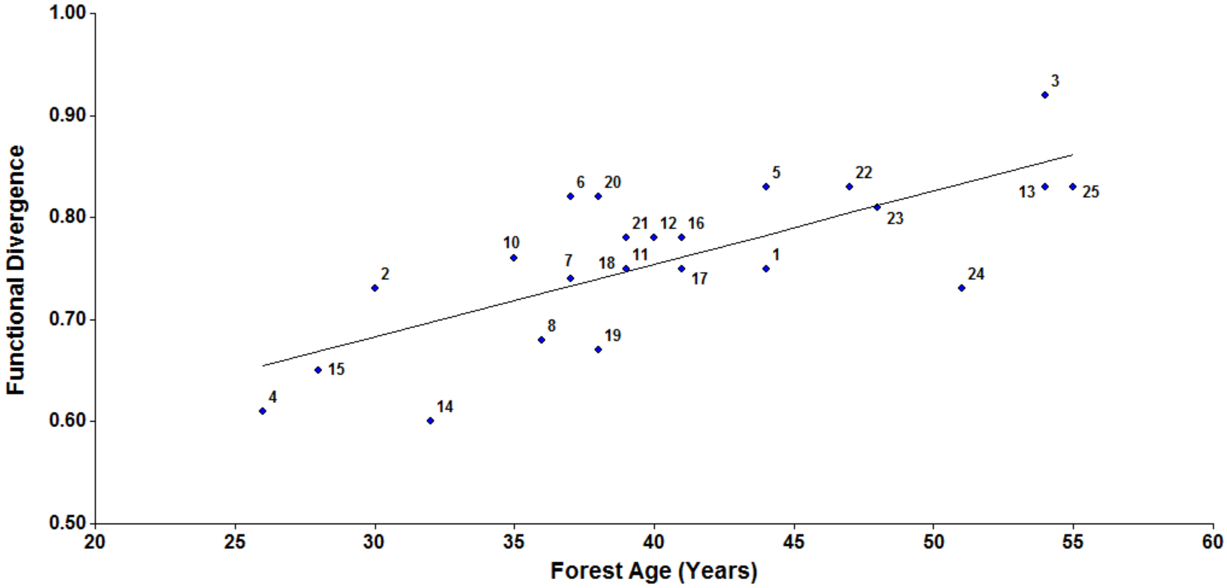


Figure Ch3- 3 Relationship between forest age and leaf dry matter content (R^2= 0.26, P= 0.0103) of saplings along the 25 0.25 ha plots of secondary forest.

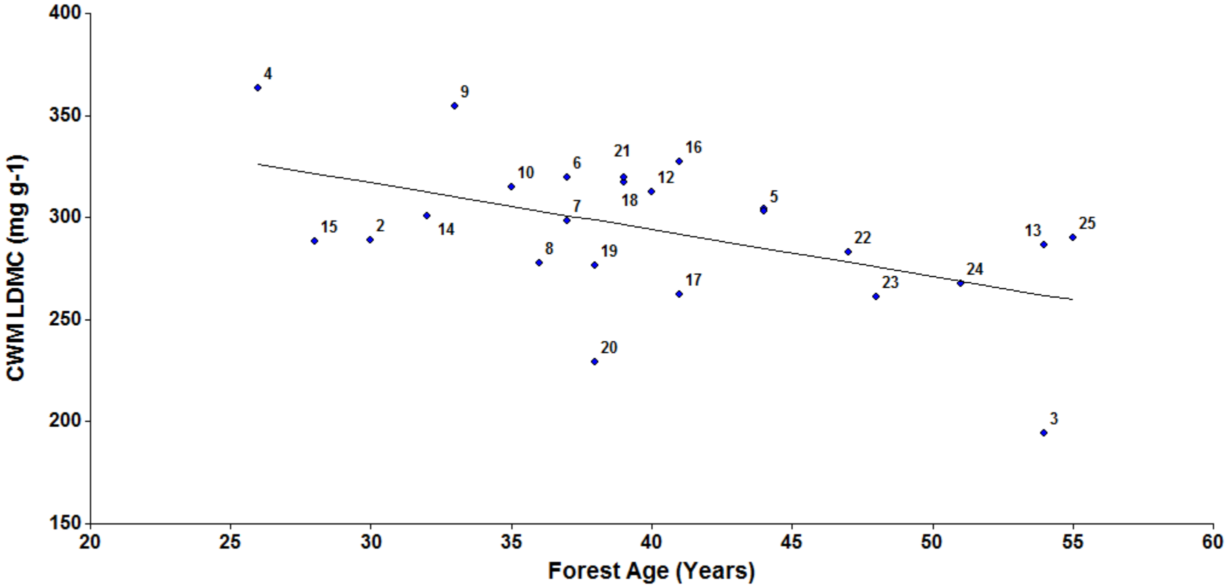
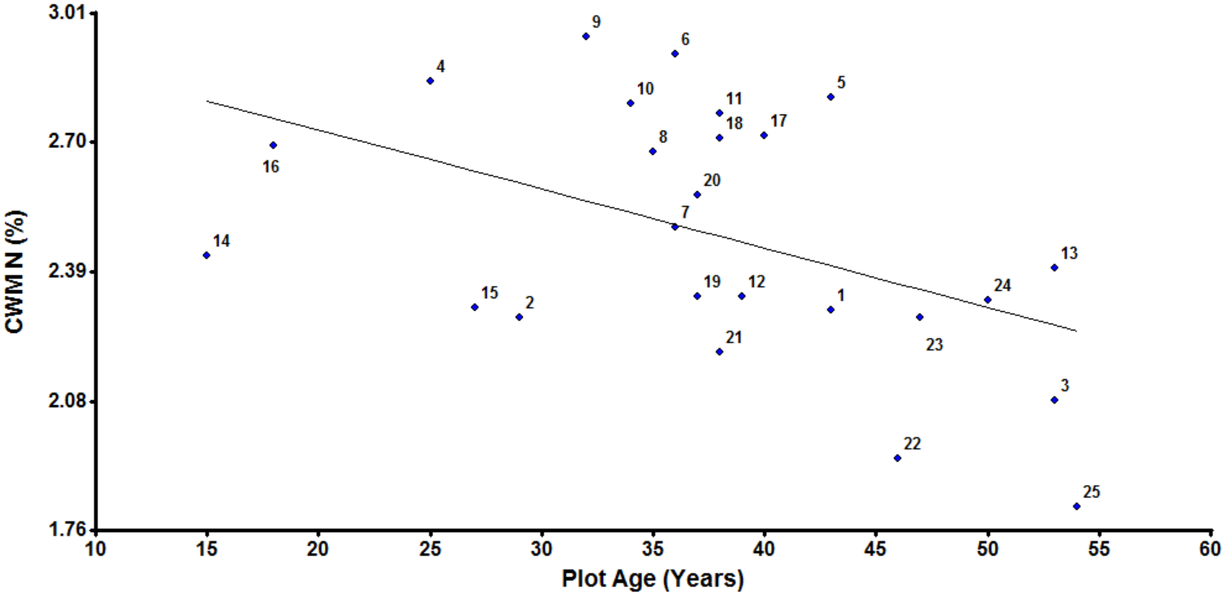


Figure Ch3- 4 Relationship between forest age and nitrogen content (R^2= 0.28, P= 0.0070) of saplings along 24 0.25 ha plots of secondary forest.



Chapter 4: Coupled social and ecological outcomes of agricultural intensification in Costa Rica and the future of biodiversity conservation in tropical agricultural regions

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Abstract

Tropical ecosystem conversion to agriculture has caused widespread habitat loss and created fragmented landscapes composed of remnant forest patches embedded in a matrix of agricultural land uses. Nontraditional agricultural export (NTAE) crops such as pineapple are rapidly replacing multiuse landscapes characterized by a diverse matrix of pasture and smallholder crops with intensive, large-scale, monoculture plantations. Using an interdisciplinary approach, we conduct a case study to examine the coupled social and ecological implications of agricultural intensification in this region, with larger application to regions experiencing similar patterns of agricultural intensification. Guided by frameworks from both political and landscape ecology, we: (1) describe the social and economic implications of pineapple expansion, specifically the concentration of land, labor and financial resources, (2) quantify pineapple cultivation's spatial characteristics, and (3) assess the effects of pineapple expansion on surrounding forest ecosystems, on the agricultural matrix and on biodiversity conservation. Our results indicate that pineapple production concentrates land, labor, and financial resources, which has a homogenizing effect on the agricultural economy in the study region. This constrains farm-based livelihoods, with larger implications for food security and agricultural diversity. Landscape ecology analyses further reveal how pineapple production simplifies and homogenizes the agricultural matrix between forest patches, which is likely to have a negative effect on biodiversity. To offset the effects of pineapple expansion on social and environmental systems, we recommend developing landscape level land use planning capacity. Furthermore, agricultural and conservation policy reform is needed to promote landscape heterogeneity and economic diversity within the agricultural sector. Our interdisciplinary research provides a detailed examination of the social and ecological impacts of agricultural intensification in a tropical landscape, and offers recommendations for improvement relevant not only to our study region but to the many other tropical landscapes currently undergoing non-traditional agricultural export driven agricultural intensification.

Introduction

Tropical forests cover less than 23% of the earth's terrestrial surface, but contain over 50% of its biodiversity and provide essential ecosystem services to the entire globe (Mace et al., 2005). As human populations continue to grow, the demand for food has driven an increase in croplands from an estimated 400 to 1800 million hectares (ha) globally (Lambin et al., 2003). Recently, much of this growth has occurred in tropical regions (Gibbs et al., 2010). The conversion of tropical ecosystems to agriculture has caused widespread habitat loss and created fragmented landscapes composed of remnant forest patches embedded in a matrix of agricultural land uses. In recent years, a new pattern has emerged whereby pasture and smallholder cropping systems are rapidly being replaced by monoculture plantation agriculture (Brannstorm, 2009; Meyfroidt et al., 2014; Rudel et al., 2009b). Impacts of the expansion of agricultural intensification[1] on social and ecological systems are not well understood, but preliminary studies suggest that intensive plantation agriculture may drive demographic and economic change in local human communities (Hecht et al., 2005; Brannstorm, 2009) and affect the structure and function of remnant forest (Tscharntke et al., 2012) and landscapes (Fahrig et al., 2011).

A primary driver of the expansion of agricultural intensification in the tropics is the increased production of non-traditional 2 agricultural export (NTAE) crops (Thrupp, 1995; Morton et al., 2006; MEA, 2007; Galford et al., 2010). From a policy standpoint, NTAE crop production is viewed as an opportunity for raising farm incomes in developing countries in the tropics, which have the attraction of low labor costs and an extended growing season (Thrupp, 1995). Tropical countries therefore now dominate global NTAE production (FAO, 2011), and NTAE crops have become a major driver of economic globalization by closely linking tropical agricultural producers to consumers in temperate locations.

While NTAEs have the potential to positively affect rural economic conditions and livelihoods, their effects on biodiversity conservation are largely negative. NTAEs are generally produced on a large scale, to accommodate greater mechanization and to maximize profits. These increases in productivity ultimately stimulate more demand for land, rather than incentivizing individuals and firms to spare land for conservation (Lambin and Meyfroidt, 2011). Therefore, NTAE production can result in simultaneous agricultural intensification and expansion, a process which homogenizes the agricultural matrix, reduces total forest cover in the landscape, and increases the isolation of native plant and animal species in remnant forest patches (Rudel et al., 2009a). This sequence of events challenges the linearity of the ‘intensification-land sparing’ hypothesis (Matson and Vitousek, 2006). This hypothesis states that agricultural intensification increases production efficiencies and creates jobs, and therefore may decrease the need for additional deforestation for agricultural expansion, reducing pressure on surrounding ecosystems (Matson and Vitousek, 2006; Grau and Aide, 2008). However, the social, economic and ecological consequences and tradeoffs of intensification differ substantially by the type and scale of the production system (Tomich et al., 2001). This context dependence underscores the importance of evaluating the socio-ecological impacts and tradeoffs of NTAE-driven agricultural intensification in specific regions throughout the tropics.

Although the ecological impacts are not well understood, intensively managed monoculture plantations with high agrochemical inputs can exacerbate biodiversity loss (Tilman et al., 2002; Ormerod et al., 2003; Jackson et al., 2012; Karp et al., 2012), impede native species’ movement across the landscape (Vaughan et al., 2007), increase habitat fragmentation (Morton et al., 2006), and degrade soil and water quality (Hyden et al., 1993; Polidoro et al., 2008). However, it may be possible to retain the economic benefits derived from intensive plantation agriculture’s productivity increases while reducing negative impacts on surrounding ecosystems. For example, practices such as retaining live fences, scattered trees, and riparian corridors within agricultural fields can enhance some components of biodiversity in agricultural landscapes (Harvey et al., 2006; Chazdon et al., 2009a). In some cases, these changes also lead to higher yields or economic returns, indicating that complementary goals of maintaining ecological integrity and agricultural production may be possible (Harvey and Villalobos, 2007; Robson and Berkes, 2011; van Vliet et al., 2012).

To identify policy and management options that allow for continued rural development and increases in agricultural productivity while mitigating impacts on tropical ecosystems, we need a better understanding of the relationships between NTAE production, agricultural intensification, and biodiversity conservation (Harvey et al., 2006). Such complex problems require an integrated, interdisciplinary approach that recognizes the interdependence of social, economic, and ecological processes inherent in the system (Eigenbrode et al., 2007; Ostrom, 2007; Botey et al., 2014). Here, we utilize such an approach. We first employ a political ecology (PE) analysis to examine the socio-economic implications of intensification from the perspective of local actors in the San Juan-La Selva (SJLS) region in Costa Rica, a rapidly developing agricultural zone where important conservation areas also exist. We then utilize landscape ecology (LE) to quantify and discuss the ecological implications of the composition and configuration of the dominant land cover types in the SJLS region with a special focus on pineapple, the dominant NTAE.

Our ultimate goal is to describe the social and ecological impacts of intensification in this system that are also relevant to other tropical regions where agricultural intensification is now occurring due to NTAE production. Our specific objectives are to: (1) describe the social and economic implications of pineapple expansion, specifically the distribution and concentration of land, labor and financial resources, (2) quantify the spatial characteristics of pineapple cultivation as a landscape component, and (3) assess pineapple expansion's effects on forest ecosystems and on the potential contributions of the agricultural matrix to biodiversity conservation. We conclude by exploring the policy implications of our integrated findings.

Theory

Integrating political ecology and landscape ecology

From this PE perspective natural resource access, use, and control cannot be understood without critically examining how land, labor, and financial resources are distributed among actors (Blaikie and Brookfield, 1987; Turner and Robbins, 2008; Peet et al., 2011). We draw from PE by utilizing stakeholder testimony to develop a qualitative chain of explanation to link sociopolitical drivers of change to local environmental and social outcomes and to assess the tradeoffs and consequences of agricultural intensification among different actors (Robbins, 2004; Turner and Robbins, 2008).

The field of landscape ecology integrates methods from ecology and geography to address questions about the effect of landscape patterns on ecological processes (Turner, 2005). One focus of LE is determining how the composition and spatial configuration of land uses and cover types affect the amount of biodiversity the landscape can support, and the associated amount of ecosystem services that are provided to humans (Turner, 2010; Fahrig et al., 2011; Wu, 2013). Previous studies indicate that some agricultural land use types are frequently used by native species for foraging, breeding, or simply as stepping stones to reach the next habitat patches (Kupfer et al., 2006; Fischer and Lindenmeyer, 2007; Harvey and Villalobos, 2007; Chazdon et al., 2009a; Gilbert-Norton et al., 2010; Vilchez Mendoza et al., 2014). Landscapes that are more heterogeneous, both in composition and configuration, are more likely to include these land use types, and therefore more likely to provide habitat and habitat connectivity for a variety of species than more homogenous landscapes (Daily et al., 2003; Fischer and Lindenmeyer, 2007; Milder et al., 2010; Fahrig et al., 2011).

Combined, PE and LE offer a holistic understanding of human modified landscapes and link ecology to the social and political implications of environmental change. A PE perspective demonstrates how political, economic, and social dynamics operating across multiple scales produce spatially explicit social and environmental change. The LE analysis quantifies the extent and ecological implications of that environmental change across the landscape. PE and LE thus inform each other and illuminate novel opportunities for sustainable agricultural production and biodiversity conservation in agricultural frontiers.

Materials and methods

Study region

The study region (616,615 ha), was delimited by available remote sensing imagery and the Nicaraguan border (Fig. Ch4- 1). It includes the landscapes within and surrounding the San Juan-La Selva (SJLS) biological corridor in northeastern Costa Rica (centered at 10.618 N, 84.138 W, Fig. Ch4- 1). This region has a mean annual temperature of 26.5 8C and annual precipitation ranging from 3000 to 4500 mm (Grieve et al., 1990; McDade et al., 1994), and lies within a wet tropical forest life zone (sensu Holdridge et al., 1975). Old- and second-growth forest remnants currently cover an important proportion of the land area (Morse et al., 2009; Fagan et al., 2013; Section 4 in this paper), retaining high tree species diversity and showing quick regeneration rates (Guariguata et al., 1997; Schedlbauer et al., 2007; Chazdon et al., 2009b; Norden et al., 2009; Sesnie et al., 2009; Bouroncle and Finegan, 2011). Soil types are generally acidic (pH 4.5), primarily Inceptisols and Ultisols (Sollins et al., 1994). The terrain is composed of low hills and mountain slopes that range from 0 to 2696 m in elevation with steep ravines in upper elevation areas, while lowland areas are characterized by alluvial terraces and flood plains that range from 0 to 400 m in elevation (Sesnie et al., 2009). These soil types and the lowland terrain are well suited for the cultivation of crops, like pineapple, that require well-drained acidic soils. The most common pineapple variety planted in the SJLS region, MD2, grows well in soils with 4.5–5.5 pH and slopes <15% (Barrientos and Porras, 2010).

The land use and land cover change history in the SJLS region reflects a recent pattern in the tropics where intensive agriculture followed initial human colonization and associated deforestation (Lambin et al., 2003). The opening of the SJLS region in the 1970s and 1980s drove massive deforestation; redistributive land reform led to the eventual dominance of smallholder farms and pasturelands (Butterfield, 1994; Schelhas and Sánchez-Azofeifa, 2006). In the late 1980s, the policies driving this land rush officially ended, replaced by policies simultaneously encouraging forest conservation and NTAE expansion (Schelhas and Sánchez-Azofeifa, 2006).

One of these policies, the 1996 Forestry Law of Costa Rica, instituted a national ban on primary forest clearing; this theoretically ‘‘froze’’ remaining forest patches on the landscape (Watson et al., 1998; Morse et al., 2009). The Law also established an incentive system of payments for ecosystem services to encourage landowners to protect primary forest, allow forest regeneration and plant trees (Evans, 1999). To further protect the remaining forest in the region, a committee established the SJLS biological corridor initiative in 2001. The boundaries of the 246,608 ha corridor were delimited to include areas that retained significant primary forest cover and spanned the gap between Indio Maíz Biological Reserve in Nicaragua and Braulio Carrillo National Park in Costa Rica. Together, these protected areas and the SJLS biological corridor form an important link in the larger Mesoamerican Biological Corridor, an initiative begun in 1997 to facilitate regional ecological connectivity from Mexico to Panama while also promoting sustainable development and improving Mesoamericans’ quality of life (IEG, 2011).

The primary policy change driving NTAE expansion during the same time period was Costa Rica's participation in Structural Adjustment Programs (SAPs). During SAP reforms Costa Rica restructured its agricultural policies away from protectionist, state-supported production of smallholder food crops toward a liberalized, globalized model promoting NTAE production and direct foreign investment (Edelman, 1999). The SAPs and more recent free-trade agreements with the European Union, the United States and now China continue to drive the expansion of NTAEs such as pineapple, citrus, and melon (Thrupp, 1995; Vagneron et al., 2009), and the decline of in-country production of food crops (Edelman, 1999). Pineapple expansion, similar to the early banana expansion in the 1990s south of the SJLS biological corridor (Vandermeer and Perfecto, 2005), influenced social and demographic changes in communities of the SJLS region. Employment opportunities at these plantations drew migrants from both Costa Rica and Nicaragua. As a result, Sarapiquí County, which covers most of the SJLS biological corridor (Fig. 1), has the fourth highest population of Nicaraguan immigrants in Costa Rica and the second highest population growth rate of all counties in Costa Rica (INEC, 2011). The growth of economic opportunities has led to some gains in economic welfare, such as increased television and car ownership (Table Ch4- 1). However, farm ownership has not increased substantially, and other analyses demonstrate the population of farmers who own and work their own farm has decreased along with the population earning their primary income from the agricultural sector (Rodriguez and Avendaño, 2005).

The study region is a critical conservation area where 43.8% forest cover is maintained with demonstrated resilient forest dynamics despite population growth and a modernizing agricultural landscape (Letcher and Chazdon, 2009; Norden et al., 2009; Schedlbauer et al., 2007; Bouroncle and Finegan, 2011; Fagan et al., 2013). These factors make the SJLS region an appropriate site to assess the effects of NTAE-based agricultural intensification on rural economies and biodiversity conservation, and to explore the tradeoffs between parallel agricultural growth and conservation objectives.

Political ecology analysis

From September 2011 to May 2013 we conducted thirty-five semi-structured interviews applying the comprehensive approach (Kaufmann, 2011; Sibelet et al., 2013). Participants in our sample were selected to include a wide range of individuals and organizations involved in land use decisions and policy in the study region, including farmers' organizations, large landholders, conservation organizations and regional and national agricultural government officials. Interviews lasted 1–2 h and were conducted in both Spanish and English. Large landholders were purposively sampled across the study region and represented the range of land cover types in the SJLS biological corridor, from forested tourism reserves to pineapple plantations. All interviewees were asked to describe the factors and policies that influence land use or their business operation decisions in particular, to describe the scale and operation of their farming system or business, and to reflect on social-environmental change in this region. The interviews were digitally voice-recorded, fully transcribed and then coded in ATLAS Ti for themes drawn from PE related to land, labor and financial resource distribution, and perceptions of agricultural and environmental change and vulnerability. In addition to the interviews, we reviewed census data, peer-reviewed publications, and gray literature in both Spanish and English. Where district-level (Puerto Viejo, La Virgen and Pital) data were unavailable, county level data were used (San Carlos and Sarapiquí counties, Fig. 1). Where county-level data were unavailable, data were derived from analyses of the entire Huetar Norte region, which includes San Carlos and Sarapiquí counties as well as the counties of Guatuso, Los Chiles and Upala (Fig. Ch4- 1).

Landscape ecology analysis

Several historical land cover maps are available for the SJLS region (Morse et al., 2009; Fagan et al., 2013). Recently, Fagan et al. (2013) used Landsat (30 m resolution) imagery to produce land cover maps for 1986, 1996, 2001, 2005, and 2011. In this study we used 2011 RapidEye multispectral satellite imagery (5 m resolution) and extensive ground truth points to produce the most high-resolution land cover map to date of the region.

Low cloud-cover RapidEye images were chosen from a 2010 to 2011 library of images. For each image, we calculated ten spectral indices based on the red edge band (Schuster et al., 2011) and a texture band based on a 7 X 7 pixel window from the Normalized Difference Red Edge Index (Appendix A). All layers were stacked to obtain a 17-band image, which was then classified in ENVI 4.7 (Exelis, Inc., McLean, VA, USA) using a support vector machine classification algorithm. Training data were obtained from 3000 ground truth points gathered from sources across the region by Sesnie et al. (2010), and Fagan et al. (2013). We classified 12 dominant land cover types (Fig. Ch4- 1). Old-growth forests are forested areas that have not been cleared during recent colonization events and exhibit a different spectral signature than forested areas known to be a product of regeneration within the past 30 years. Although this forest may have been impacted by selective logging, understory clearing or hunting, the resultant composition and structure is not distinctive from original primary forest with its canopy emergent trees canopy palms, lianas and native understory species. (Sesnie et al., 2009). Forest remnants corresponds to forest patches that are smaller than 2 ha in total size. New forests include both secondary growth, including all stages of natural regeneration, and native tree plantations (Guariguata et al., 1997). Exotic tree plantations mainly include species such as *Tectona grandis* and *Gmelina arborea*. Agricultural land cover types are pasture, banana, pineapple, perennial crops [e.g. peach palm (*Bactris gasipaes*), black pepper (*Piper nigrum*)] and annual crops. Urban areas, water, and bare soil are the remaining land cover types. Several forest classes exhibited spectral overlap, thus to improve classification we first classified all forest within the RapidEye images into a single category, and then subdivided this category into distinct forest types from the Landsat-based map developed by Fagan et al. (2013). Overall accuracy for the 2011 land cover maps is 94%, with different values for each land cover category (Appendix B). Accuracy was assessed using an independent set of 513 ground-truth points gathered in 2011; this data set was not used for image classification purposes.

To assess landscape composition and measure the effects of agricultural land uses on forest fragmentation, we selected a set of metrics related to area, contrast and aggregation available in the FRAGSTATS spatial statistics program (V.4.2, University of Massachusetts, Amherst, MA, USA) (Appendix C, Table C1). Metrics were selected based on their universality and consistency as independent components of landscape structure at the class and landscape level as identified by Cushman et al. (2008) and McGarigal et al. (2012). We then calculated all metrics within and outside the biological corridor separately (Fig. Ch4- 1). More detailed information on the FRAGSTATS analysis is given in Appendix C.

Additionally, we conducted an analysis in Arc Map 10.1 (ESRI, 2011) to compare the amount of fine-scale landscape elements such as single trees, live fences, and riparian corridors, that are present in pineapple plantations versus other agricultural land cover types. These fine-scale habitat features cannot be identified using lower-resolution (30 m Landsat) imagery; the availability of high-resolution (5 m RapidEye) maps provides a new opportunity to assess the contributions of these fine-scale features to forest connectivity and to determine which land cover types are most likely to retain these features (Boyle et al., 2014). To quantify the fine-scale landscape features in each land cover type in the SJLS region, we used a tree cover map based on 5 m RapidEye and the zonal statistics tool in ArcMap 10.1. Considering single trees and groups of trees with a size <0.5 ha, we calculated the mean percentage area covered by trees for the entire area of each individual land cover type: pineapple, annual crops, perennial crops, banana and pasture.

To understand the potential growth boundaries of pineapple, we calculated the percentage of the SJLS biological corridor and surrounding landscape that is suitable for its cultivation. We used the following criteria to identify optimal land for pineapple cultivation: (a) slope of less than 15%, (b) characterized by Inceptisol or Histosol soils, and (c) occurring within 3 km of a well-developed (i.e., paved or well-maintained dirt) road (Enríquez, 1994; Pitácuar, 2010). Slope, soil type and distance from an improved road were obtained using layers from the Atlas of Costa Rica (ITCR, 2008). Although these are agro-ecological criteria for pineapple production, their use is supported by an economic analysis conducted in the SJLS biological corridor that verified pineapple production is the most profitable land use and consistently occurs closest to major road networks when compared to other crops, pasture and forest (Pitácuar, 2010).

Results and discussion

Our findings link spatial patterns of land use in the study region to historical and current economic policy, and reveal the impacts of pineapple expansion on both social and ecological systems. Our LE analyses indicate that the study region (Fig. Ch4- 1) is dominated by pasturelands (39%), old-growth forest (34%) and new forest (9.1%) (Table Ch4- 2). Pineapple plantations and patches of bare soil (likely including land in preparation for agricultural uses) respectively cover 3.6% and 2.9% of the landscape. The rest of the landscape is occupied by other types of agricultural lands, tree plantations, urban areas and small (<2 ha) patches of remnant forest; each of these land cover types represents between 2.1% and 0.72% of the landscape (Table Ch4- 2).

Pineapple expansion and intensification as a social, economic and ecological process

As illustrated in Fig. Ch4- 2, pineapple was almost non-existent in the landscape in 1986, around the time of the SAP reforms, but increased markedly by 1996 and showed the greatest expansion from 2001 to 2011. This pattern of expansion was not limited to the SJLS region; from 2006 to 2010 the land area across Costa Rica used for pineapple cultivation doubled from 22,400 ha to 45,000 ha while the crop export value increased 55% (Barquero, 2011). By 2011, pineapple had become the second most important agricultural export for Costa Rica (worth $666 million in 2010) and had created 27,000 direct jobs and 110,000 indirect jobs in production, harvesting, and processing (Barquero, 2011). Nicaraguan immigrants are the principal labor force for the majority of these unskilled jobs, where wages range from $1.20 to $2.00 per hour (Acuña-González, 2009). Although field interviews confirmed these wages are comparatively better than in less regulated sectors of the agricultural economy (i.e., cassava) and migration for work is the primarily pull to this region, the work in pineapple plantations is physically demanding, results in high exposure to pesticides, and can have low job and wage security especially for undocumented workers (ILRF, 2008; Acuña-González, 2009; Shaver, 2014). Nearly 50% (22,138.9 ha) of the total national land area in pineapple lies within our study region. Fagan et al. (2013) found that pineapple production in the SJLS region from 2001 to 2011 was largely not replacing old-growth forest, but was instead expanding primarily into lands previously used for pasture or annual and perennial crops such as cassava, peach palm, and ornamental plants, as well as young regenerating forests, which experienced high rates of clearing during this time period.

In the SJLS region, pineapple plantations currently occupy a higher percentage of total land than traditional agricultural production systems including annual and perennial crops (Table Ch4- 2). Although pineapple plantations cover less than 4% of the total study region, they usually occupy large patches, second in size only to pasture and forest patches (Table Ch4- 2). Of total land dedicated to pineapple plantations in the study region, 78% occurs outside the SJLS biological corridor and 22% lies within (Table Ch4- 3). Outside the corridor, pineapple patches are 10 ha larger on average and more aggregated than those found within. Pineapple's more aggregated spatial configuration relative to other crops (Tables Ch4- 2 and Ch4- 3) illustrate how pineapple homogenizes the agricultural matrix, converting smaller farm parcels and pasturelands into large-scale plantations.

Our pineapple suitability analysis suggests that this trend of homogenization is likely to spread across more of the landscape, especially if road development continues at its current pace. We found that in the entire study region, 26.2% of the land is highly suitable for pineapple cultivation and an additional 15.7% is moderately suitable (Fig. Ch4- 3). Considering only land within the corridor, currently 2% is under pineapple cultivation (Table Ch4- 4). However, 17.1% is highly suitable for future pineapple cultivation and an additional 16.6% is moderately suitable. Both our suitability analysis and current economic trends (Fold and Gough, 2008; Vagneron et al., 2009) suggest future pineapple production will likely expand both within and outside of the corridor.

In addition to changing the composition and configuration of land cover types, pineapple is also driving a social economic shift within the agricultural sector away from smallholder crops and toward intensive, large-scale, agribusiness-dominated production systems (Table Ch4- 4). The NTAE sector's social and economic organization is related to cost advantages associated with larger scale operations that favor agribusinesses and inhibit smallholder participation (Table Ch4- 4). For example, in the Huetar Norte region, the average investment to begin planting pineapple is $9900/ha (Villegas et al., 2007). In an area where the median monthly income of agricultural households is $625, this investment capital requirement is prohibitive for most households (Programa Estado de la Nación, 2010). Furthermore, in a survey of pineapple producers in the northern part of the corridor, Piñero and Díaz Ríos (2007) found it cost small and medium pineapple producers between 0.036 and 0.013 cents to produce 1 kg of fruit whereas it cost large producers 0.003 cents. When the last pineapple census was conducted in 2004, pineapple farms in the Huetar Norte region with less than 10 ha accounted for only 12.9% of the land in pineapple production, while farms larger than 100 ha accounted for 76.8% (MAG census, 2005). These large farms range in size from 200 to 1200 ha, with an average of 492 ha under cultivation (Villegas et al., 2007). In our FRAGSTATS analysis (Table Ch4- 3), the largest patch of pineapple outside the SJLS biological corridor was 5466 ha and the largest within the corridor was 2308 ha; this suggests individual pineapple plantations are large and tend to border each other to form contiguous mega-patches of pineapple across the landscape.

The market structure of the pineapple sector also favors largescale plantations over small pineapple farms. The pineapple variety MD2 is densely planted, and the proportion of labor done by hand requires a large, year-round hired labor force. Conventional pineapple cultivation relies on high agrochemical and infrastructural investments (Table Ch4- 4), an expense most small farmers cannot afford (Piñero and Díaz Ríos, 2007). Large agribusinesses is vertically integrated in this sector (i.e., it dominates all stages of production and market distribution) (Lee et al., 2012), or fulfills contracts for a larger company, typically Dole or Del Monte, who together control 85% of all pineapple exported from Costa Rica (Vagneron et al., 2009; Blacio et al., 2010; Amanor, 2012). This market structure favors economies of scale and is high risk for smallholders who are easily outcompeted by larger companies (Piñero and Díaz Ríos, 2007; Lee et al., 2012).

Local government officials in the SJLS biological corridor are aware of how large agribusinesses dominate pineapple production and of how untenable pineapple is as a primary rural development strategy for small farmers. A Ministry of Agriculture representative remarked, ‘‘With MD2, there was an explosion of big producers . . . some small and medium farmers also got involved who were in other crops, were in livestock, tubers or palm and they got into pineapple. Why? Because in 2003–2008, it was profitable. There were good prices, costs were good, but with the 2008 crisis which erupted in the U.S. . . . followed [by] Europe in the years 2010–2012 . . . we were in a bad situation, and people moved away from the activity, especially smallholders.’’

Several times interviewees described land conversion to pineapple as a duel process of concentrating land and reducing smallholder land ownership. A prominent farmer and rancher’s organization leader explained ‘‘Many farmers who produced not only cattle but also tubers, very few of them changed their activities to grow pineapple because those that had 50 hectares or less – in pineapple that is very little – so many of them sold their land to [pineapple] companies and have left the activity [farming].’’ For example, one of the larger pineapple plantations in the region covers 1500 ha, 43% of which is rented land from neighboring farms. This trend of ‘land grabbing’ has been documented in pineapple in Ghana (Amanor, 2012) as well as for other NTAEs like oil palm in southern Costa Rica (Piñero and Díaz Ríos, 2007). Although, this may provide immediate rent-based income for smallholders or income in the short term from the sale of their land, often small farmers struggle to transfer into another profession due to low education and professional experience. These losses of control either in land use decision-making or in land ownership are often detrimental in the long term as they can lead to land degradation and foster insecurity in the rural poor through dependency on wages and commodity booms that are typically temporary and unsustainable ecologically and economically (Amanor, 2012).

In reflecting on the social and environmental change caused by the expansion of pineapple, different stakeholders have distinct interpretations of how pineapple expansion plays into the larger vision of rural development. Stakeholders interested in sustainable development for both local farmers and local biodiversity often expressed concern about the economic and ecological vulnerability to pineapple expansion. As one representative of the SJLS biological corridor initiative said ‘‘I have a very encompassing vision of sustainability and I see that the pineapple scheme is not what is going to make the country advance in the theme of sustainable development or for the local people. We are betting on an export product that in any given moment the market changes, at an international level, the next day it is going to be Philippines or Ecuador or Hawaii. . . If the prices fall, the farmers here will be left in complete ruin because they are not owners of their farms, many times they sell or rent, lose control of the production, they lose control of their land and they all have big loans for machines, fertilizers and costly technology packages. It is a very big risk and for [forest] connectivity it is fatal.''

In contrast, a pineapple company manager saw this expansion increasing employment and therefore development in an economically marginalized region. He explained, ''Always, this type of company [agribusiness] brings development. For example, with 400 ha someone can handle more or less 300 cows. To handle 300 cows, they have to employ about three people. Pineapple needs one person per half hectare. That is to say, yes it brings development.'' One of the largest forest landowners in the region reiterated this idea that pineapple companies develop the region and facilitate economic growth: ''the town was here, but it was a very small town. There was no economic activity to speak of, I mean, a lot of people were just living off their land . . . when these pineapple guys came here, they improved a lot of stuff. They had the money to improve roads, they had the money to talk to politicians and bring infrastructure in here, I mean, you see now in this area, a lot of nice pick-ups driving around – those are people that sold land for a good price here, so a lot of stuff has changed here.'' These diverging descriptions demonstrate that people living and working in this landscape have conflicting ideas about a desirable path to development in this region and the long and short-term benefits of pineapple. This rural development model, with its emphasis on large-scale production of pineapple and exclusion of smallholders, demonstrates the tradeoffs between national economic objectives for export growth and job creation and regional issues of equity, household food security and rural poverty alleviation (Tomich et al., 2001).

On a global scale, large agribusiness prevalence and smallholder exclusion do not always characterize NTAE crop production. For example, prior to 2000, the majority of the fresh pineapple imported to the European Union (E.U.) came from West African countries, where smallholder production and smallholder integration into the value chain predominated (Fold and Gough, 2008). The primary reason pineapple production in Costa Rica has not followed a similar pattern is Del Monte's dominance in its market, which until 2003 held the exclusive patent to the MD2 pineapple variety. This monopoly excluded initial smallholder participation in the production boom and consolidated the pineapple value chain into the hands of large agribusinesses (Fold and Gough, 2008). MD2s recent introduction in Ghana is driving a shift from smallholder to agribusiness production systems, resulting in land concentration, increased dependence on wage labor for agricultural livelihoods, and prohibitive production costs for smallholders (Fold and Gough, 2008; Amanor, 2012). As these aspects of the ‘Costa Rican’ model of pineapple production continue to be replicated globally in other NTAE crops, other regions may also experience similar changes to socio-economic characteristics and landscape composition.

Impacts of pineapple expansion on forest and future biodiversity conservation in the agricultural matrix

Given the proportion of original forest cover remaining, the study landscape can be categorized as fragmented (Table Ch4- 2; McIntyre and Hobbs, 1999). However, results from FRAGSTATS analysis indicate the remaining old-growth forest is not highly subdivided, as the aggregation metrics SPLIT, PROX, ENN and LPI show (Table Ch4- 3); the largest old-growth forest patch covers almost 7% of the total study region (Table Ch4- 2). In accordance with the original criteria selected to establish the SJLS biological corridor, our results show that more than half of the total old-growth forest cover within the SJLS region is located within the corridor limits, and in contrast to the landscape outside the SJLS biological corridor, forest remnants within the corridor are considerably larger and less isolated (Table Ch4- 3).

These results confirm the findings of Morse et al. (2009) and Fagan et al. (2013) that showed the 1996 Forestry Law and the system of payment for ecosystem services have been successful in promoting conservation of old-growth forest in this landscape. The matrix between these forest patches continues to change, though, and the assessment of how these changes affect remaining forest should become a priority.

Previous studies document that forest directly adjacent to agricultural land uses suffers from ‘‘edge effects’’, which drive changes in forest microclimate, tree mortality, and in the abundance and distribution of animal species; the severity of edge effects vary depending on the type of adjacent land use (Fischer and Lindenmeyer, 2007; Schedlbauer et al., 2007; Bouroncle and Finegan, 2011; Laurance et al., 2011). FRAGSTATS metrics such as core area (CORE), which describes the patch area free of edge effects, and edge contrast indices (TECI), which describe the proportion of forest edge in maximum contrast (Table A1), are useful metrics for assessing the impact of edge effects. TECI is based on the dissimilarity in vegetation structure between two adjacent land cover types; for example, new forest and old-growth forest would have low contrast values, whereas pineapple and old-growth forest would have high contrast values. When higher contrast land covers, such as bare soil, pineapple, or pasture are adjacent to forest, it reduces the core area of the forest patch that is free of edge effects (CORE) (Table Ch4- 3). In the SJLS biological corridor there is a high incidence of old-growth forest patches that border high contrast land covers like pasture or pineapple and are thus vulnerable to strong edge effects (Table Ch4- 3).

Euclidian distance to the nearest patch of the same type (ENN) and the proximity index metric (PROX) are also useful for assessing how old-growth forest patches are affected by the agricultural matrix (Table Ch4- 5). A low value of the proximity metric indicates that the patch is more isolated and has more forest fragmentation in its surroundings (Whitcomb et al., 1981). Our results reveal that old-growth forest patches sharing a border with pineapple have higher ENN values and lower PROX values than similar patches bordered by pasture (Table Ch4- 5), meaning that the patches surrounded by pineapple are dramatically more isolated. Interestingly, old-growth forest patches that share a boundary with pineapple have a larger mean area than those surrounded by pasture (Table Ch4- 5). This is due to differences in production strategies between pasture and pineapple. Pastures often retain small old-growth forest patches, groups of trees, and riparian areas, which serve to provide water and shade for livestock. In contrast, pineapple plantations seek to maximize continuous planted area, and therefore retain the old-growth forest patches protected by law but eliminate single trees or groups of trees within the production area, which can be important for connectivity. The isolating effect of pineapple on forest patches is a concern that conservation interests in the corridor identified. One reserve owner noted, ‘‘We have a small [forested] area that depends on the larger [protected] areas to have a diversity of organisms . . . we want to generate connectivity so that we do not become converted into an island surrounded by pineapple.’’ Furthermore, Fagan et al. (2013) found that between 2001 and 2011 pasture was three times more likely to revert to natural secondary regeneration than were croplands, including pineapple.

Although the new forests land cover type occupies more than 55,000 ha in the landscape, the high number of patches (NP) of small mean size (AREA) with low mean proximity values

(PROX) to other similar patches indicates that this type of vegetation cover is subdivided and isolated (Tables Ch4- 2 and Ch4-3). The new forest land cover type is equally distributed outside and within the SJLS biological corridor, but within the corridor, patches are less subdivided and represent a higher percentage of the total land area (Table Ch4- 3). Within this land cover type, later stages of secondary growth are known to have different species composition but similar vegetation structure and tree species richness to old-growth forest (Finegan, 1996; Guariguata and Ostertag, 2001), and provide habitat for species of conservation concern (Fischer et al., 2006). Using high-resolution imagery allowed us to detect small (<2 ha) old-growth and new forest patches not detected in previous studies using Landsat imagery (Fagan et al., 2013). These small forest patches grouped within the forest remnant land cover type represent a very low percentage of the landscape, but potentially serve as stepping-stones to enhance forest connectivity (Harvey et al., 2005; Hanson et al., 2007). For example, Hanson et al. (2008) found long-distance gene flow can be maintained among separated populations of canopy tree species through the connectivity stepping-stones of isolated trees or small forest patches provide.

Results of our analysis of fine-scale landscape features indicate that, among all land covers types analyzed, pineapple has the lowest percentage of tree cover per unit area, with the exception of banana plantations (Fig. Ch4- 4). The greatest differences in tree cover were observed between pineapple and perennial crops, such as peach palm or fruit trees and pasture, which have twice the percentage of tree cover (3.9–4.7%) than pineapple plantations. Another important difference between pineapple versus pasture or perennial crops is the spatial distribution of tree cover. In pasture and crops, single trees and small groups of trees are retained within the land use rather than just at the edges, as in pineapple (Fig. Ch4- 4). A pineapple producer explained the practice of maintaining only legally mandated tree cover within the plantations. There is a river that cuts across the plantation, and as he said, ‘‘I have to leave 60 meters or 30 meters on each side [of the river] and that makes lot[s] of hectares. Over there – there is a spring and with a spring you have to leave 1000 meters around it. So that’s how they form patches of forest. There are patches all over but when you combine them it’s a lot of forested land.’’ The practice of retaining forest cover only along riparian corridors is evident in Fig. Ch4- 4, where it can be seen that trees in pineapple plantations (a) are confined to depressions or river corridors within the plots, leaving most of the plantation void of tree cover.

In contrast, trees in pasture (b) are usually dispersed across a large area, creating patches of low and high tree density and maintaining heterogeneity within this land use.

Land cover types characterized by having either more scattered trees and live fences (Perfecto et al., 2003; Vaughan et al., 2007; Harvey et al., 2008), or vegetation structure that is more similar to natural forest cover (Brotons et al., 2003; DeClerck et al., 2010; Prevedello and Vieira, 2010; Eycott et al., 2012; Vílchez Mendoza et al., 2014), are more likely to be used by wildlife for foraging, breeding, or as stepping stones to reach other habitat patches (Kupfer et al., 2006; Fischer and Lindenmeyer, 2007; Harvey and Villalobos, 2007; Chazdon et al., 2009a; Gilbert-Norton et al., 2010; Vílchez Mendoza et al., 2014). The reduced tree cover within pineapple plantations and the pronounced difference in vegetation structure between pineapple and natural forest suggest that pineapple likely reduces habitat availability and connectivity when compared to other land cover types such as pasture or annual and perennial crops.

The SJLS region retains a significant proportion of old-growth forest cover, but our analyses show conversion of smallholder crops and pasturelands to pineapple plantations affects forest cover, leading to loss of total tree cover and of landscape heterogeneity. Furthermore, our pineapple suitability analysis suggests that if road development and favorable market conditions continue, pineapple plantations will further spread into the SJLS biological corridor. These findings emphasize the importance of developing effective policies to mitigate current and future impacts of pineapple expansion on the linked social and ecological systems in the study region.

Current policy on pineapple at a landscape scale

Policy discussions about the future of pineapple in Costa Rica have been occurring at the national level through the National Pineapple Platform (Plataforma Nacional de Piña – PNP), which is a two-year participatory dialog hosted by the United Nations Development Program, the Ministry of Agriculture and the Ministry of the Environment. Participants in this dialog have developed an action plan for 2013–2017 (http://www.pnp.cr/plan. php), focusing mostly on actions to improve practices at the farm level; an issue the leaders in the SJLS biological corridor initiative have identified, ‘‘There are management standards but they are focused completely on the plantation; there is no vision of the landscape.’’

Municipalities are also important players in forming policies to regulate pineapple. They have legal power to develop a territorial land use-zoning plan called a ‘‘plan regulador’’ which can direct where pineapple expands and limit its growth if desired. This plan is the best mechanism municipalities have to effectively partition public and private land and exclude certain land uses or developments, but most rural municipalities do not have current or well-developed plans (Pérez Pelaez and Alvarado Salas, 2003). ‘‘Sometimes, there are not sufficient resources to do studies, because of this they [municipalities] get behind a bit . . . so until they do the studies, they cannot determine legally, under their land use zoning plan, what is the zone for this [X] land use,’’ explained a representative of the National Environmental Technical Secretariat (Secretaría Técnica Nacional Ambiental).

Conclusions

Our results reveal how pineapple expansion produces social and environmental change with local conservation implications. In particular, our synthesis of data suggests that pineapple concentrates land, labor, and financial resources on the landscape, thereby increasing the homogeneity of the agricultural economy in the study region. When spatially heterogeneous pastures with tree cover or smallholder farms are converted to monoculture plantations dominated by agribusinesses, the loss of autonomy (i.e., land ownership or land use decision-making) constrains farm-based livelihoods, food security and agricultural diversity.

Pineapple production also simplifies and homogenizes the agricultural matrix between forest patches. It further isolates old-growth forest patches, and reduces total tree cover, all of which are critical for maintaining connectivity of remnant forest patches. Since biodiversity in agricultural landscapes is positively associated with percent of tree cover and landscape heterogeneity, the continued spread of pineapple plantations is likely to have a negative effect on biodiversity conservation.

Despite pineapple’s negative influence on some social and ecological components of the landscape, in some ways the SJLS region represents a best-case scenario. Strict and innovative regulatory and incentive schemes have successfully promoted retention of old-growth forest cover, and pineapple is just beginning to dominate agricultural land use. Spatially heterogeneous smallholder production systems and pasture with tree cover are still abundant within the corridor and contribute to forest connectivity.

To protect biodiversity and promote inclusive rural development in the face of pineapple expansion we propose several landscape-level policy and management approaches. First, management approaches should implement plans that have already been developed. In the SJLS region there has been unprecedented interinstitutional dialog and coordination to develop an action plan for sustainable pineapple production, which is summarized in the PNP action plan. Second, policies that encourage landscape-level planning (Sayer et al., 2012) should be established to promote land use heterogeneity and economic diversity within the agricultural sector. Retaining smallholder agriculture as a viable livelihood should be a priority for both conservation and agricultural policy makers, as smallholders are critical contributors to rural poverty alleviation, food security, landscape heterogeneity and crop diversity (Dahlquist et al., 2007; Perfecto and Vandermeer, 2008; Tscharntke et al., 2012). Third, landscape level planning should follow national level policies such as the Costa Rican 2021 carbon neutrality goal. This goal has already motivated several multinational agribusinesses to establish carbon neutral production strategies (Kilian et al., 2012). Agribusinesses could also commit to retaining more forest cover within plantations or to forest offset programs; this would contribute to their goals of offsetting carbon emissions while also increasing habitat connectivity. However, any investments toward carbon neutrality or sustainable production by agribusinesses need to be matched throughout the value chain by retailers in marketing and setting higher selling prices to offset these investments. Fourth, the Forestry Law of 1996 should be updated to more effectively target conservation and restoration of both riparian and secondary forest to promote increased habitat connectivity (Fremier et al., 2013) and move Costa Rica closer to its goal of carbon neutrality. Current conservation regulations in Costa Rica protect old-growth forest, while creating perverse incentives that block regrowth of secondary forest (Sierra and Russman, 2006; Morse et al., 2009; Fagan et al., 2013) despite evidence that secondary forests contribute to carbon sequestration (Pan et al., 2011).

Due to the global relevance of balancing local economic growth with biodiversity conservation, this Costa Rican case study can serve as a model against which to compare other regions currently undergoing rapid expansion of NTAE crop production. Indeed, understanding the social-ecological impacts of agricultural intensification in tropical regions is a critical piece of promoting the sustainability of rural agrarian development around the world. As shown in this study, landscapes operate as integrated social-ecological systems, and must be managed holistically to retain spatially and economically diverse land uses that support sustainable rural livelihoods and create a balance between agricultural production and biodiversity conservation.

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Tables and Figures

Table Ch4- 1. Basic indicators of economic welfare, population composition, and population size in districts that cover the area of the SJLS biological corridor, 1984 and 2011[a].

Districts	1984			2011		
	Puerto Viejo	La Virgen	Pital	Puerto Viejo	La Virgen	Pital
Television ownership	19	8	75	4469	2676	3823
Car ownership	11	20	51	871	727	1159
Farm ownership	336	456	513	442	345	646
Domestic wood or charcoal use	607	822	1015	455	417	348
Nicaraguan immigrants	341	193	181	5249	1701	4114
Population (total)	4107	4451	6614	20,174	10,706	17,325

[a] All values are numbers of individuals. Puerto Viejo and La Virgen are in Sarapiquí County, while Pital is in San Carlos County. These 3 districts cover most of the area of the SJLS biological corridor (see Fig. 1). CCP Census Data (CCP, 2011; http://ccp.ucr.ac.cr/) are presented as number of individuals.

Table Ch4- 2. FRAGSTATS analysis results summarizing area and subdivision metrics for all land cover classes in the San Juan-La Selva region. Metric units are given in parenthesis, and a detailed definition of each metric is available in Appendix C, Table C1. Land cover categories are listed from highest to lowest according to their total area in the landscape.

Land cover	Area				Subdivision		Isolation	
	CA (ha)	PLAND (%)	LPI (%)	AREA (ha)	SPLIT	NP	PROX	ENN (m)
Pasture	244,959	39.7	12.3	57	45	4299	337,372.10	84
Old-growth forest	210,022	34.0	6.7	50	105	4185	28,891.80	120.9
New forest[a]	56,448	9.1	0.1	6	160,503	10,120	113.4	141.6
Pineapple	22,139	3.6	0.9	33	7017	672	25,759.70	241.9
Bare soil	17,968	2.9	0.1	6	248,864	3290	127.5	273
Perennial crop	13,259	2.1	0.1	6	337,451	2291	259.6	238.7
Banana	8919	1.4	0.6	29	21,397	312	1571.60	968.2
Annual crop	7815	1.3	0.1	5	268,389	1462	625.7	379.2
Exotic tree plantation	6609	1.1	0.04	4	1,551,421	1528	43.4	455.8
Urban	4565	0.7	0.1	5	1,298,114	980	246	329.3
Forest remnant	4424	0.7	0.001	1	56,602,757	3088	5.5	429.3

CA: total area, PLAND: percentage of landscape, LPI: largest patch index, AREA: mean patch size, SPLIT: splitting index, NP: number of patches, PROX: proximity index, ENN: mean Euclidean nearest-neighbor distance.

[a] This land cover type includes secondary growth and native tree plantations.

Table Ch4- 3. Comparison of the spatial characteristics of dominant land cover types both within (245,008 ha) and outside (371,607 ha) of the San Juan-La Selva biological corridor. Metrics units are given in parenthesis. Core area and contrast metrics are given only for old-growth forest.

	Metric	Old-growth forest	New forest[a]	Pasture	Pineapple
Within	PLAND (%)	47.2	11.3	32.0	2.0
	LPI (%)	13.7	0.1	3.0	0.9
	AREA (ha)	76	6	37	26
	SPLIT	33	44,863	269	9892
	PROX	47,516	129	22,451	9659
	ENN (m)	94	123	87	407
	CORE (ha)	62			
	TECI (%)	57			
Outside	PLAND (%)	25.3	7.7	44.7	4.6
	LPI (%)	7.6	0.1	13.3	1.1
	AREA (ha)	30	5	59	33
	SPLIT	146	142,119	36	4552
	PROX	10,596	92	253,769	20,329
	ENN (m)	128	156	80	197
	CORE (ha)	22			
	TECI (%)	63			

AREA: mean patch size, CORE: mean core area per patch, ENN: mean Euclidean nearest-neighbor distance, LPI: largest patch index, PLAND: percentage of landscape, PROX: mean proximity index, TECI: total edge contrast index: mean edge contrast index, SPLIT: splitting index.

[a] This land cover type includes secondary growth and native tree plantations.

Table Ch4- 4. Comparison of different production system variables demonstrating that intensification occurs across multiple components of a production system and shifts the socio-economic organization of agricultural production[a].

Component of the production system	Smallholder farm	Extensive cattle ranch	Agribusiness pineapple plantation
Labor type and intensity	Family labor	Family and hired labor: 0.001 person-days/ha.	Hired labor: 0.5 person-days/ ha.
Cost of production	Varies; most costly product is pepper at $2500/ha	Low	High (average $9900/ha for international export) up to $22,000/ha for organic production[b]
Use of inputs	Varies	Low	High (average of 1000 kg/ha/yr of fertilizer); uses machinery, continuous production
Land cover type	Diversified, often including subsistence food crops and remnant trees	Pasture, sometimes with remnant trees and live fences. Density: 1–3 cow/ha.	Monoculture Density: 72,000 plants/ha
Average size	0.9–6 ha	35 ha	492 ha
Market destination	Sold at national farmers' markets, to packing plants or to intermediaries at farm gate	Sold at regional auctions for international export or for national consumption	Exported internationally to major supermarket chains via direct contracts
Principal reason for land use	Low investment, easy market accessibility, low technical/ labor requirements.	Easy market accessibility, low labor requirements, culture	Price, international demand

[a] Interviews 2011–2013. Smallholder data: Sáenz-Segura et al. (2007); MAG (2005). Pineapple data: FAO (2007). Cattle data: Holmann et al. (2008). All data are for the Huetar Norte region (see Fig. 1).

[b] Organic production is more costly than conventional production due to increased labor and production costs (e.g. manual weeding/pest management, covering fields in plastic), limited availability of research on optimal production techniques and plant varieties, and lower yields per hectare.

Table Ch4- 5. Mean patch area and isolation metrics for forested land cover classes.

	All patches			Share boundary with pasture (n=3559)			Share boundary with pineapple (n=402)		
	AREA (ha)	PROX	ENN. (m)	AREA (ha)	PROX	ENN (m)	AREA (ha)	PROX	ENN (m)
Old-growth forest	57	28,892	121	29	31,459	115	44	3202	176
New forest[a]		113	142						
Forest remnant		6	429						

[a]This land cover type includes secondary growth and native tree plantations. AREA: mean patch size, PROX: proximity index, ENN: mean Euclidean nearest-neighbor distance.

Figure Ch4- 1 The San Juan-La Selva biological corridor and surrounding areas are located in northeastern Costa Rica. High resolution Rapid Eye imagery from 2011 was used to identify 12 major land cover types. New forest land cover type includes secondary growth and native tree plantations.

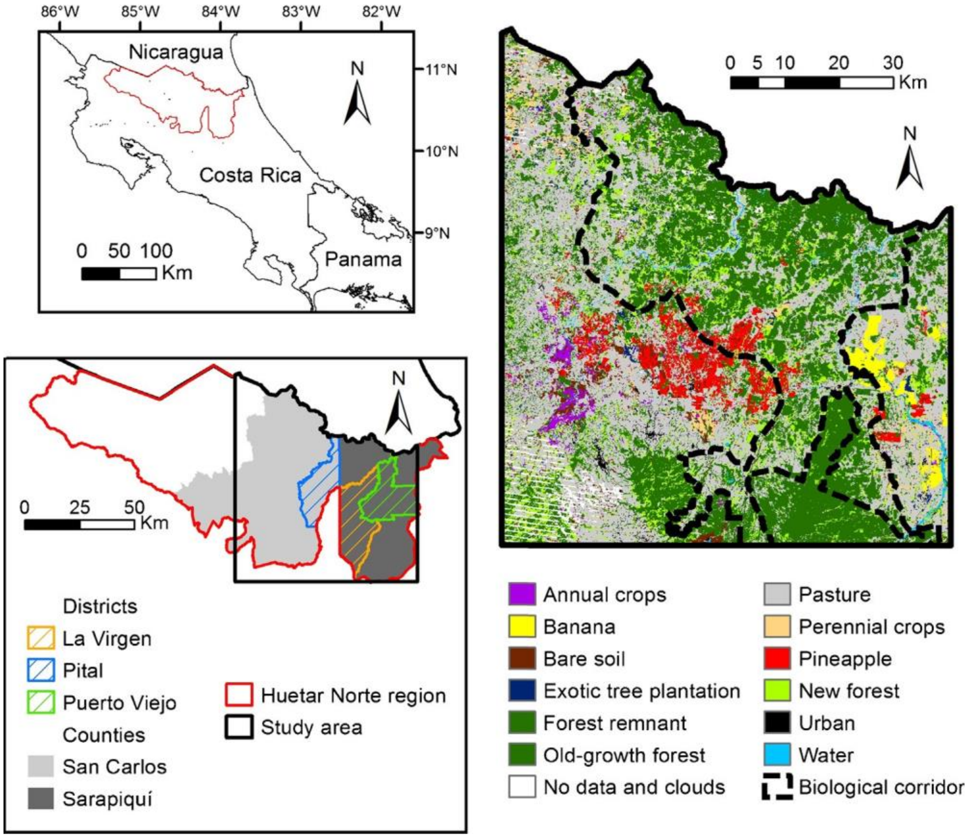


Figure Ch4- 2 The expansion of pineapple in the San Juan-La Selva biological corridor and surrounding landscape, 1986–2011. The 1986, 1996, 2001 and 2005 maps are from Fagan et al. (2013), and the 2011 map was produced for the current study. The legend shows major land use types and forest cover types. The ‘‘new forest’’ class includes secondary growth and native tree plantations.

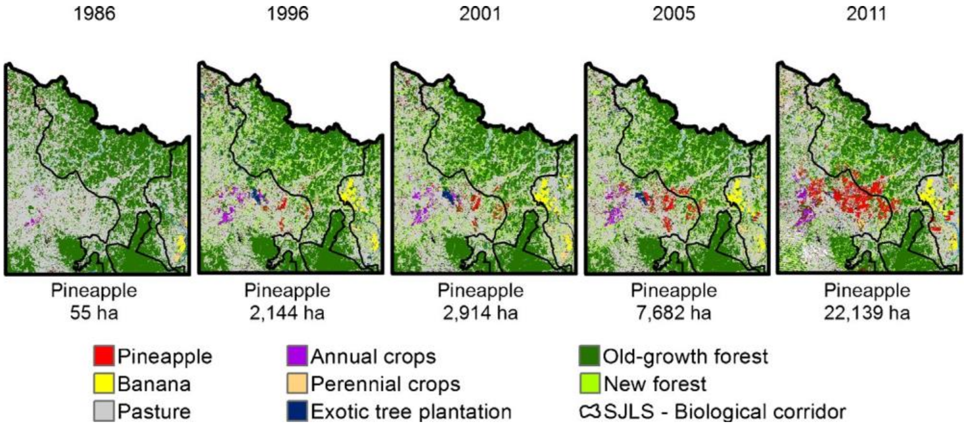


Figure Ch4- 3 Pineapple suitability analysis. Suitable areas for pineapple cultivation were identified according to soil type and slope. Because the probability of pineapple cultivation increases with accessibility to roads, a 3 km buffer (hatched area) around principal roads is also shown.

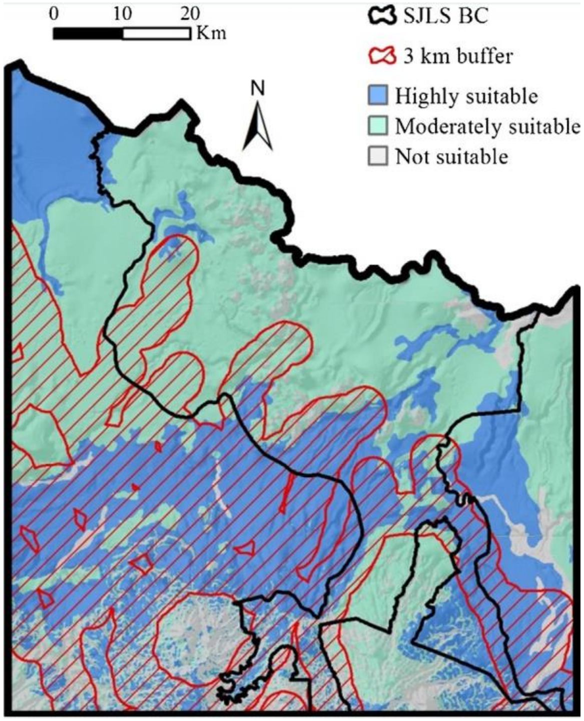
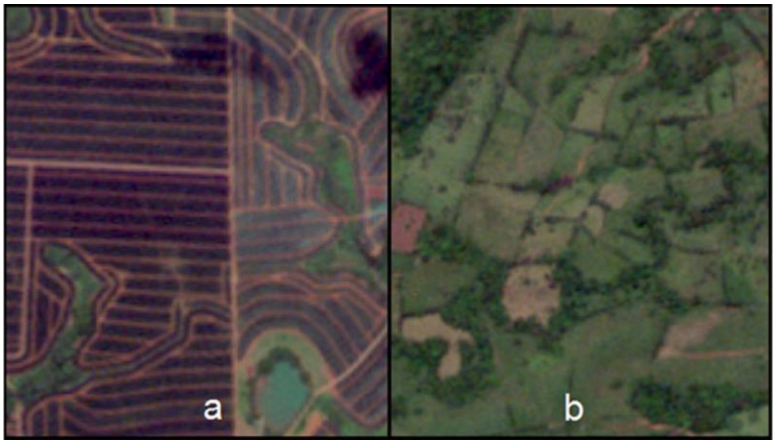
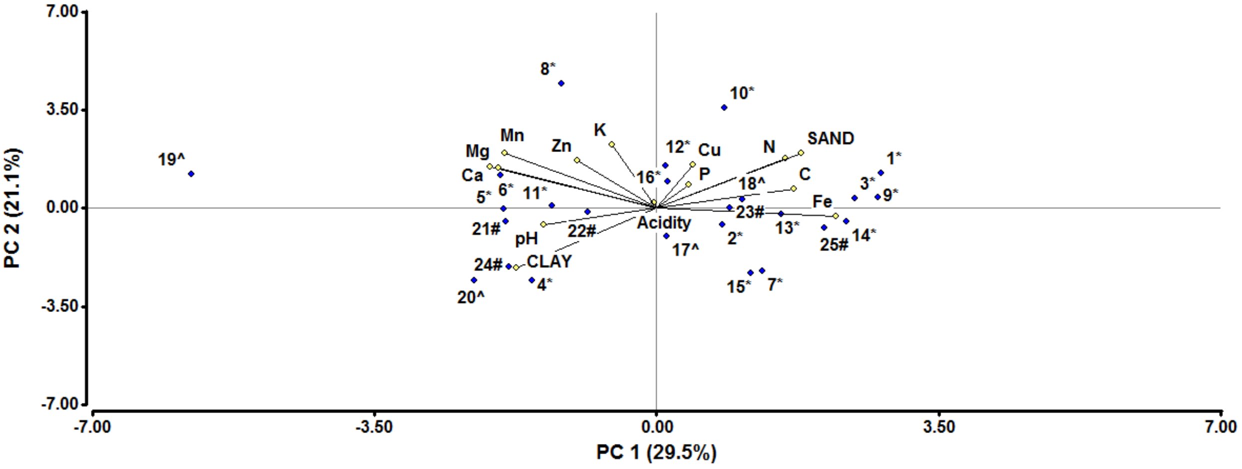


Figure Ch4- 4 Mean percentage of area covered by fine-scale forest features such as single trees, groups of trees and live fences, in the dominant agricultural land cover categories: (a) pineapple, (b) pasture. Pictures correspond to 5 m resolution RapidEye imagery. STD is standard deviation.

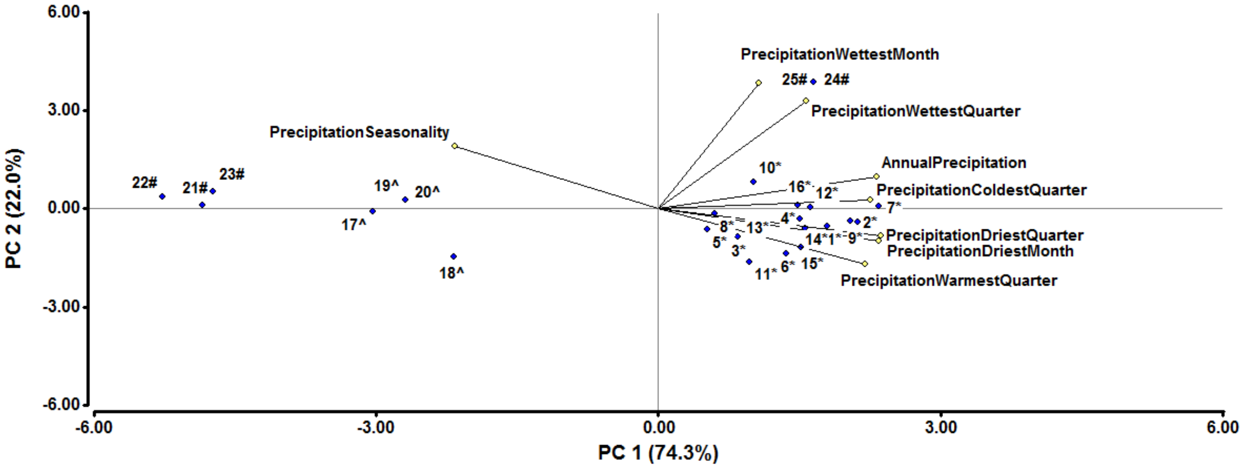


Appendix

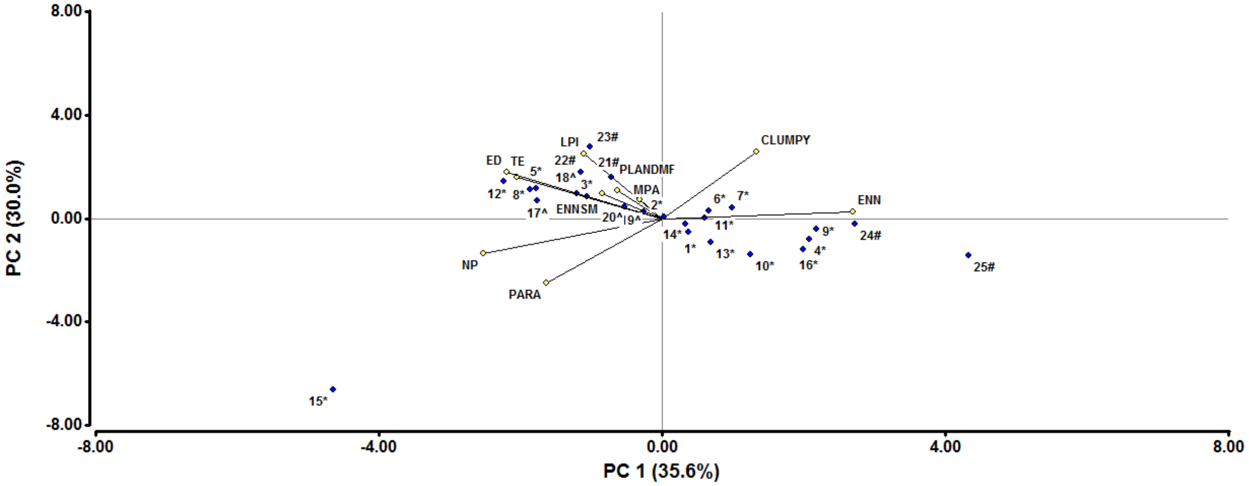
Appendix 1a. Principal Components Analysis for the soil chemical and physical properties for the 25 secondary forest patches plots. Plots are represented by blue symbols and soil properties by yellow symbols. Plots with * symbol are from landscape 1 (1-16), the symbol ^ is from plots in landscape 2 (17-20) and plot numbers with the symbol # are from landscape 3 (21-25).



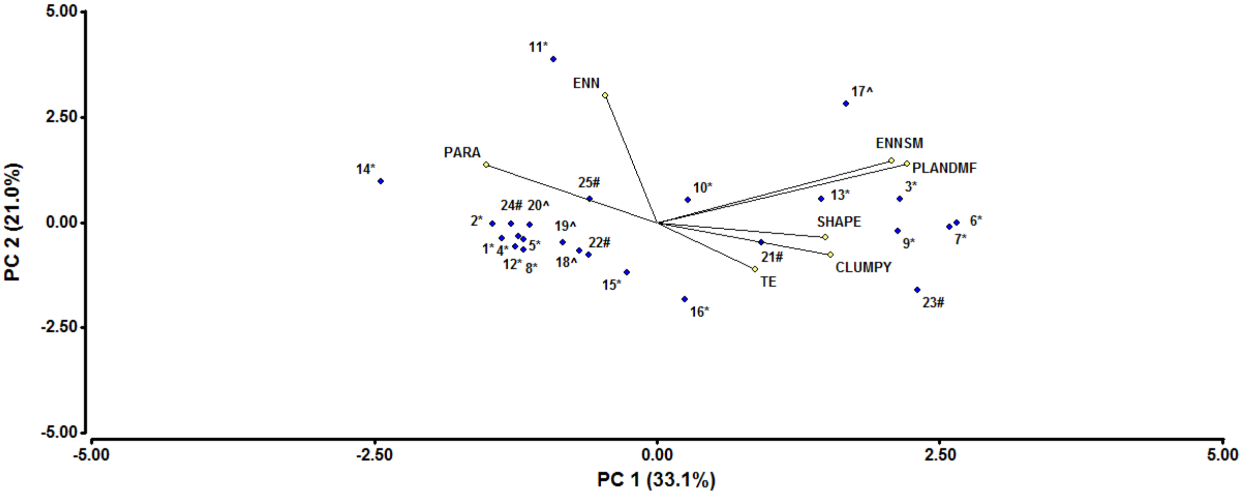
Appendix 1b. Principal Components Analysis for the precipitation variables for the 25 secondary forest patches plots. Plots are represented by blue symbols and soil properties by yellow symbols. Plots with * symbol are from landscape 1 (1-16), the symbol ^ is from plots in landscape 2 (17-20) and plot numbers with the symbol # are from landscape 3 (21-25).



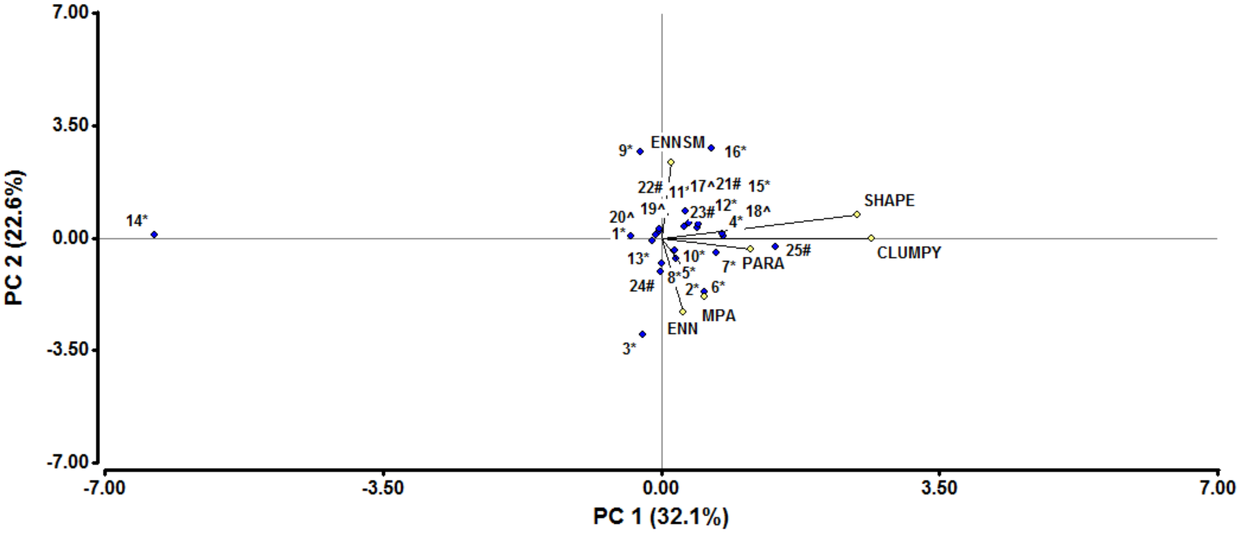
Appendix 1c. Principal Components Analysis for the landscape metrics at 5 km radii for the 25 secondary forest patches plots. Plots are represented by blue symbols and soil properties by yellow symbols. Plots with * symbol are from landscape 1 (1-16), the symbol ^ is from plots in landscape 2 (17-20) and plot numbers with the symbol # are from landscape 3 (21-25).



Appendix 1d. Principal Components Analysis for the landscape metrics at 1 km radii for the 25 secondary forest patches plots. Plots are represented by blue symbols and soil properties by yellow symbols. Plots with * symbol are from landscape 1 (1-16), the symbol ^ is from plots in landscape 2 (17-20) and plot numbers with the symbol # are from landscape 3 (21-25).



Appendix 1e. Principal Components Analysis for the landscape metrics at 500 m radii for the 25 secondary forest patches plots. Plots are represented by blue symbols and soil properties by yellow symbols. Plots with * symbol are from landscape 1 (1-16), the symbol ^ is from plots in landscape 2 (17-20) and plot numbers with the symbol # are from landscape 3 (21-25).



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