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Diversity and structure of regenerating tropical dry forests in Costa Rica: Geographic patterns and environmental drivers

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ABSTRACT

Much of the dry tropical forest biome has been converted to agricultural land uses over the past several centuries. However, in conservation areas such as those in the Guanacaste and Tempisque regions of Costa Rica, tropical dry forests are regenerating due to management practices including fire suppression. To better understand the patterns of secondary succession occurring in Costa Rican tropical dry forest, we established 60 20 × 50 m plots in mature and regenerating forests in the Sector Santa Rosa (formerly known as Parque Nacional Santa Rosa) and Palo Verde National Park. Plots were stratified into three plant communities: tropical dry oak forest (*Quercus oleoides*) (SROAK), Santa Rosa tropical dry forest (SRTDF), and Palo Verde tropical dry forest (PVTDF). In these plots we measured and identified and all individuals >10 cm DBH, measured but did not identify stems <10 cm but taller than 1.3 m, counted woody seedlings (<1.3 m height) and analyzed soil chemical and physical properties.

Soil properties clearly differentiated vegetation communities and defined a gradient from rocky, siltier soils with low nutrient availability (SROAK soils) to clayey, nutrient-rich soils (PVTDF). Soils in the Santa Rosa dry forest had intermediate soil properties compared to the other two plant communities and had the highest tree species richness. Successional dynamics as assessed from plots of different age showed that the patterns of change in indices of stand structure, species richness and tree community composition varied with forest type (and hence soil properties). Forest structure (densities of stems in different size classes) recovered to levels found in mature forest within 4–5 decades in SRTDF and PVTDF, but increased with stand age in the oak forest. In all plots, we identified 135 species from 45 families. Simple and partial Mantel tests showed that across all plots, both stand age and soil properties explain variation in species composition, but that there is also unexplained spatial variation in tree community composition after accounting for spatial co-variation with soils. Additional analyses suggested that this is due to β-diversity, i.e. changes in the regional species pool from the northern (Santa Rosa) to more southern area (Palo Verde). Species composition in young stands was dominated by wind-dispersed species in SRTDF and PVTDF, and by animal-dispersed species in the oak forest. We conclude that the management strategy of fire control promotes passive regeneration of secondary dry forest in Costa Rica. However, if a specific forest composition is desired, more active restoration strategies may be necessary.

1. Introduction

Secondary forests, typically defined as forests recovering from human-caused disturbance, are becoming an increasingly abundant and important land-cover type in tropical regions (Brown and Lugo, 1990; Finegan, 1996; Chazdon, 2003; Arroyo-Mora et al., 2005). Thus, understanding how fast the structure and composition of these forests recover, and which variables control these processes is a central question in tropical forest ecology. A complex interplay of biotic and abiotic factors is likely to affect regeneration in these forests. Biotic or management-related factors include previous land use, factors that affect seed arrival (e.g. seed sources and dispersers) and factors that affect germination and establishment (e.g. competition from remnant pasture grasses, litter layer depth, lack of mycorrhizal symbionts and seed predators) (Bazzaz and Pickett, 1980; Ewel, 1980; Wijdeven and Kuzee, 2000; Khurana

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and Singh, 2001; Hooper et al., 2005). Abiotic factors affecting regeneration include continued disturbance from fire, precipitation, temperature, availability of resources such as light and nutrients, and frequency and intensity of drought (Janzen, 1988a; Gerhardt, 1993; Campo and Vazquez-Yanes, 2004; Ceccon et al., 2004; Vargas-Rodriguez et al., 2005). Almost certainly the relative importance of these different factors in controlling the fate of abandoned agricultural lands varies among regions, forest types and with the spatial scale under consideration.

Our understanding of regeneration processes in tropical dry forests has lagged behind our understanding in tropical wet forests (Meli, 2003; Vieira and Scariot, 2006). Tropical dry forests are broadly defined as forests having a distinct dry season lasting several months with little or no precipitation (Murphy and Lugo, 1986). In addition to containing unique biodiversity and a high degree of endemic species (Trejo and Dirzo, 2002), tropical dry forests are characterized by a large functional diversity of trees, especially in terms of leaf phenological strategies (Eamus, 1999). For example, leaf habit strategies of trees range from evergreen to drought-deciduous, with intermediate strategies such as brevi-deciduous species that drop their leaves at the beginning of the dry season and then flush new cohorts.

Tropical dry forests are now considered the most endangered tropical biome (Janzen, 1988b) because much of the lands once covered by these forests have been converted to agricultural uses (Miles et al., 2006; Quesada and Stoner, 2004). The reasons for the large-scale transformation are many, but include tropical dry forest's vulnerability to fire, relatively high soil fertility, and comfortable climate (Murphy and Lugo, 1986). Despite past transformation as well as ongoing threats to tropical dry forests, significant steps towards conservation and restoration are being made, especially through the use of management practices in protected areas (Allen, 2001; Janzen, 2002). In particular, active fire prevention and/or controlled burning and grazing to reduce biomass have encouraged secondary forest regeneration in the Areas de Conservación (national conservation areas) in Northwestern Costa Rica (Janzen, 1988b; Stern et al., 2002; Barboza-Jiménez, 2002), although the benefits of cattle grazing as a management strategy have been debated (Stern et al., 2002; Quesada and Stoner, 2004). To make informed management decisions and prioritize future needs for conservation in this region, it is important to understand which biotic and abiotic factors most limit secondary forest regeneration and if management can change the trajectory and pace of succession.

To better understand the patterns and controls of secondary succession and forest composition, we studied old growth and regenerating dry forests in Northwestern Costa Rica using a network of 60 forest plots in two Areas de Conservación. We employed the commonly used chronosequence approach of identifying stands that differ in age, measuring forest structure and composition, and then inferring regeneration dynamics by assuming a space-for-time substitution. Our study differs from previous studies in this region (Kalacska et al., 2004) in that we consider forest age as a quantitative variable, sampled over a wider range of forest types, and emphasize how regeneration dynamics depend upon edaphic variables.

Forest plots in a region may share similar tree species because they have similar environmental conditions (e.g. soils and geomorphology), similar ages and/or disturbance history (Leduc et al., 1992; Urban et al., 2002). Alternatively, similarity may be due to other factors such as the pool of species that are able to disperse into any specific area. Many of the factors that affect forest composition may be spatially correlated (i.e. pairs of samples located closer together are more similar than pairs of distant samples). Because of this spatial autocorrelation, identifying the relative importance of different controls on succession and community composition requires differentiating the direct co-variation between species distributions and environmental or land-use history variables, versus indirect co-variation due spatial autocorrelation among the drivers of forest composition (Legendre and Fortin, 1989; Urban et al., 2002; Reynolds and Houle, 2003; Goslee et al., 2005). To accomplish this, we compared the composition and structure of forest plots across gradients of soil characteristics and stand age, and then used partial Mantel tests and path analysis to partition variation in forest composition into components due to different, potentially interacting factors. Because both soils and vegetation communities are known to vary across the dry tropical forest biome in Costa Rica (Hartshorn, 1983; Winters, 1995; Gillespie et al., 2000), we focused on how successional patterns and edaphic factors vary within three distinct forest types found in two conservation areas, Sector Santa Rosa (formerly known as Parque Nacional Santa Rosa) and Parque Nacional Palo Verde, located in two conservation areas. Although the nature, duration and intensity of previous anthropogenic disturbances may affect secondary succession and forest recovery (Uhl et al., 1988; Lawrence, 2004), in some forests such as the ones we studied is it difficult if not impossible to establish definitive land-use histories. Our approach to accounting for this potential source of variation was to sample intensively within the study areas, while also acknowledging that land-use history (aside from stand age) is an important, uncontrolled factor in our dataset.

2. Methods

2.1. Site description and history

This study was carried out in Sector Santa Rosa, formerly known as Parque Nacional Santa Rosa Parque Nacional Santa Rosa (referred to as Santa Rosa throughout the text) located in the Area de Conservación Guanacaste (10.84°N, 85.62°W, established in 1971) and Parque Nacional Palo Verde (referred to as Palo Verde) located in the Area de Conservación Tempisque (10.35°N, 85.35°W, established in 1977) in Northwestern Costa Rica, which span much of the original extent of the Costa Rican dry tropical forest biome (Fig. 1) (Holdridge et al., 1971). Santa Rosa has a mean annual temperature of 25 °C, mean annual precipitation of 1575 mm with a range from is 880–3030 mm (based on a 26-year record from Instituto Meterologico Nacional and investigadoresacg.org/), and a 6 month dry season (Gillespie et al., 2000). Palo Verde National Park has a mean annual temperature of 25 °C, mean annual precipitation from 1267 to 1717 mm (with a range from 714 to 2130 mm), and a 5 month dry season (Gillespie et al., 2000; www.ots.duke.edu).

Soils in this region are largely Inceptisols of volcanic origin (unpublished soil map) and some Vertisols. According to local soil maps available from the parks, our sites in Santa Rosa lie on Typic Ustropepts and to a lesser extent on Lithic Ustropepts. The upper plateau areas of Santa Rosa have poor rocky soils derived from pumice and ash (Hartshorn, 1983). Below the plateau of Santa Rosa is a heterogeneous landscape consisting of steep forested slopes, small intermittent stream valleys, and lowlands with deeper, largely basalt derived soils (Hartshorn, 1983). The forested uplands of Palo Verde are characterized by a series of porous limestone hills. Soils range from thin rocky soils along the ridges to lowlands with deeper soils derived from a mix of limestone and clay or silt deposits from the nearby Tempisque River (Hartshorn, 1983). The plots we sampled at Palo Verde were on two of the most abundant soil types Typic Pellusterts/Typic Pelluderts and Typic Ustropepts (unpublished soil map; www.ots.duke.edu).

The tropical dry forests of Northwestern Costa Rica contain several distinct plant communities with varying percentages of evergreen

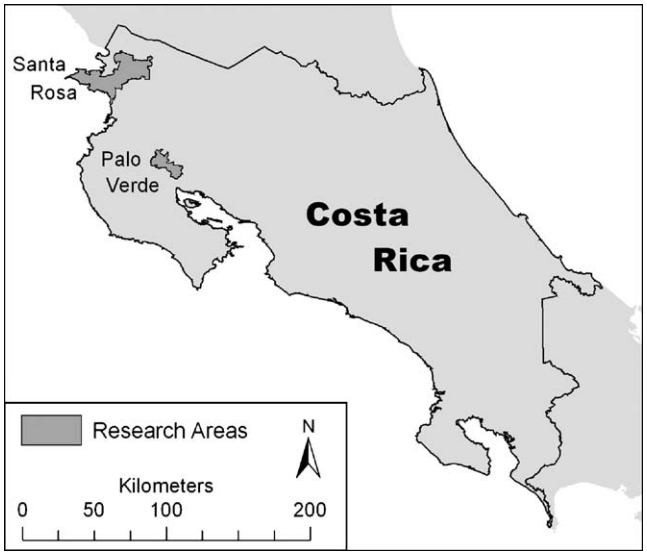

Fig. 1. Approximate locations of study sites within Costa Rica.

and deciduous species. Among other vegetation types, Santa Rosa contains both evergreen forests dominated by live oak, *Quercus oleoides*, (referred to throughout the text simply as oak) and more typical, species-rich tropical dry forest (Hartshorn, 1983). The oak forest exists on pumice/ash soils and extends from the Santa Rosa plateau to the base of nearby volcanoes with an elevation range of 280–800 m (Klemens et al., 2008). Although dominated by oak, these forests also contain a large number of other species that co-occur in the adjacent mixed deciduous forest where oaks are rare (Boucher, 1981, 1983). On the hill slopes and in the lowlands of Santa Rosa, the forests are more diverse and have varying degrees of deciduousness ranging from about 20% evergreen hillsides to almost completely evergreen lowlands (Janzen, 1986). Palo Verde forests also contain deciduous and evergreen tree species and include large areas of flooded forests (that we did not study). Evergreen oak forests are absent in Palo Verde.

While archaeological, pollen and charcoal data suggest humans have lived in this region for thousands of years (Lange, 2006; Piperno, 2006), pre-Columbian population densities were likely low and the extent to which these early people modified the environment and affected forest species composition is unknown. In general, following the arrival of the Spanish in the 1500s, indigenous populations declined (Quesada and Stoner, 2004); however, starting in the 1800s and intensifying through the 1900s both areas experienced large-scale conversion from a forest-dominated landscape to a savanna-pasture landscape maintained through fires and grazing (Boucher, 1983; Quesada and Stoner, 2004). Only small patches of the original tropical dry forest remain today (Janzen, 1986). Exotic grasses (mainly *Hyparrenia rufa*) were introduced along with livestock (Daubenmire, 1972; Pohl, 1983), which suppress regeneration of native tree species largely because they resprout vigorously following fire (Daubenmire, 1972; Klemens et al., 2008). The parks included in this study were both established as protected areas in the 1970s and various management tools including fire suppression (in Santa Rosa) and cattle grazing to reduce fuel loads (in Palo Verde) have been used to facilitate forest regeneration (Janzen, 1988a; Stern et al., 2002; Quesada and Stoner, 2004).

2.2. Plot sampling

We established 60 50 × 20 m (0.1 ha) survey plots stratified by vegetation type and stand age. Although selecting the spatial locations of plots at random is often desirable in vegetation studies, human patterns of land use are not random (Sader and Joyce, 1988; Helmer, 1999; Lawrence and Schlesinger, 2001). Forested sites that are converted to agricultural uses are often chosen preferentially based upon criteria such as accessibility, soil fertility and/or proximity to markets. As our main explanatory variable of interest was stand age, we selected plots according to rigorous criteria defined below, rather than scatter plots at random across the landscape. Within each vegetation type, we identified a number of potential sites that differed in age (using a combination of methods described below) and then chose a subset of suitable plots to sample based upon accessibility and/or randomly choosing among two or three equally suitable plots by a coin toss. All plots were on fairly level slopes. Plots were not equally distributed among forest types; we sampled more plots in Santa Rosa, where we identified a larger number of potentially suitable sites (i.e. sites that were accessible and for which we were fairly confident about forest age). Sixteen plots were in upland oak forest patches in Santa Rosa (SROAK), 25 were lowland and hillside dry tropical forest in Santa Rosa (SRTDF), and 19 were in the lowland dry tropical forest of Palo Verde (PVTDF). Geographic locations of all plots were collected using a Trimble GPS receiver. Approximate stand ages were assigned to plots based upon (i) local, expert knowledge of tree age and specific site history and (ii) overlay analyses in a geographic information system with a chronosequence of both wet and dry season Landsat Thematic Mapper satellite images from 1986, 1996, 2000, and 2007. Reflectance values of areas of known age were compared to those of unknown areas using both wet and dry images of multiple years. Stand age estimates from satellite images were determined when we were certain that pasture had changed to forest in the time between 2 dates of imagery. These ages were verified with on-site assessments of tree age and local knowledge. The estimated ages of sites older than 1986 are based solely on expert knowledge, and thus our confidence in the accuracy of these estimates decreases with older stands. However, we also used the stable isotopic composition of soil carbon to corroborate these estimates (described below).

At Santa Rosa, we sampled three patches of dry tropical forest that were not previously cleared for agriculture; we refer to these as "mature" stands and have arbitrarily assigned an age of 100 to these stand for statistical analysis. We were unable to locate any undisturbed oak forest, although some oak plots did have large oak trees that were likely remnants from when the sites were grazed. At Palo Verde the oldest stands we sampled are estimated to be more than 50 years old based upon the knowledge of people who have worked in the area since before the park was established (the extent to which these sites had been disturbed before then is unknown).

Woody vegetation was sampled with a nested scheme. Within the plots we identified to species all trees >10 cm diameter at breast height (DBH, i.e. 1.3 m) and measured DBH with a diameter tape. Because we identified only those trees >10 cm DBH, we restrict our analyses and interpretations of diversity and community composition to species that had successfully established and grown to this diameter, which excludes most shrubs. We counted and measured DBH of all trees taller than breast height but <10 cm DBH along a 4 m wide transect down the center of each plot (but did not identify them). Finally, we counted all woody seedlings shorter than breast height along a 1 m transect down the center of each plot. Lianas were excluded from our sampling as were woody shrubs that did not fall into our height/diameter categories.

2.3. Soil analyses

In each plot, we collected two sets of soil samples from the top 10 cm of mineral soil (i.e. excluding the litter layer). We preferred

sampling by fixed depth rather than genetic horizon, which is appropriate for our goal of comparing quantitative measures of soil characteristics among plots (Boone et al., 1999). First, we collected three volumetric samples (192 cm^3 volume to 10 cm depth) evenly spaced along the central, long axis of the plot with a turf grass sampler. These samples were used to measure bulk density, soil moisture and stone content (defined as the weight of stones, rocks and pebbles that did not pass through a 2-mm sieve), and results are reported as plot means. Next we collected a second set of samples (also from the 0–10 cm depth of surface mineral soil) with a 2.5 cm diameter punch tube corer. For this set of samples, we extracted soil cores from the four corners of the plot and at six evenly spaced intervals along the central, long axis of the plot. The punch tube samples were composited by plot, air-dried, pushed through a 2-mm sieve, and used for chemical analyses and particle-size determination.

Soil pH in water was measured on air-dried soils in a 1:2.5 soil to solution ratio with an Oakton pH electrode. Total elemental concentrations of nutrients derived from rocks (B, Ca, Cr, Cu, K, Mg, Mn, Na, Ni, P and Zn) were measured after digestion in hot nitric acid followed by quantification with ICP-AES at the Research Analytical Lab at the University of Minnesota. Elemental concentrations are reported as mg kg^{-1} on an oven-dried weight basis (110 °C). We chose to analyze total concentrations of rock-derived elements rather than "exchangeable" or "extractable" nutrients, because, while it has been shown that different types of vegetation and land-use history can affect *labile* or *extractable* nutrient pools (Johnson and Wedin, 1997; Lawrence and Schlesinger, 2001), it is unlikely that vegetation affects *total* element pools over the timescale of our study (~60 years). Thus, total concentrations of rock-derived elements among plots are more likely to reflect differences in parent material between sites, rather than vegetation history or current species composition. In contrast, it is well established that atmospherically-derived elements in soil including organic carbon and nitrogen vary with stand age and vegetation composition (Powers, 2004). Total carbon and nitrogen were measured on a COSTECH Elemental Analyzer at the University of California, Davis and are reported as percentages on an oven dry weight basis. In addition, the stable isotopic composition of carbon, $\delta^{13}C$, was analyzed for these soil samples on a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) at UC Davis. The stable isotopic composition of soil organic carbon largely reflects the varying contributions of vegetation with the C3 versus C4 photosynthetic pathways (Martinelli et al., 1996; Powers, 2006). As such, it is a useful tracer of stand age when vegetation switches from C4 tropical pasture grasses to C3 trees (deKoning et al., 2003). Particle-size determination (percentages of sand, silt and clay) was made via the hydrometer method at the Research Analytical Laboratory at the University of Minnesota.

2.4. Data analysis

2.4.1. Edaphic variables

In order to determine whether the three forest types could be distinguished by soil characteristics, we compared soil physical and chemical properties among forest types using Welch two sample *t*-tests with three tests per variable to account for the three pairwise comparisons. The criterion for inferring statistical significance was adjusted for 57 multiple comparisons using a Bonferroni correction factor ($\alpha = 0.0009$).

2.4.2. Composition and diversity

The software program EstimateS was used to construct sample-based species accumulation curves for each forest type with the Mao Tau function, which is a sample-based approach appropriate for comparing different numbers of individuals sampled from equal sized plots (Colwell, 2005). We also computed the Shannon–Weiner index of diversity (H′), which incorporates both species richness and evenness, as a way to assess variation among stands with different ages. One young plot had only one individual tree >10 cm DBH, and thus was omitted from these calculations.

2.4.3. Partitioning variation in composition into environmental, historical and geographic components with Mantel and partial Mantel tests

Ecological applications of the Mantel and partial Mantel test have been described in detail elsewhere (Legendre and Fortin, 1989; Leduc et al., 1992; Urban et al., 2002; Reynolds and Houle, 2003; Goslee et al., 2005). In brief, Mantel and partial Mantel tests provide a statistical framework for relating two or more distance or dissimilarity matrices and assess significance via permutation procedures (Goslee and Urban, 2007). Matrices that can be used as inputs to the analysis include dissimilarity matrices (e.g. Bray-Curtis, etc.) that describe the differences in vegetation among plots in terms of species abundance or presence/absence, the geographic (Euclidean) distances among plots, and the differences among plots in terms of environmental variables (e.g. soil nutrients, soil texture, disturbance history, etc.) (Legendre and Legendre, 1998).

In applications of Mantel and partial Mantel tests in plant ecology, it is commonly assumed that "space" (i.e. the geographic locations of the plots) influences environmental, disturbance, and/or land-use history variables (i.e. soil samples collected close to one another tend to be more similar than distant samples), but not the converse (i.e. these variables do not affect the locations of sampling points in space) (Goslee et al., 2005). The relationship between explanatory variables and vegetation composition may be direct (causal) or indirect (spurious) if the correlations are due to vegetation and explanatory variables both being correlated in space.

We used the software package "ecodist" written for Splus and R (Goslee and Urban, 2007) to compute simple and partial Mantel correlations between distance matrices of space, soil variables, stand age and species composition as outlined in the hypothesized paths among variables diagrammed in Fig. 2. We used these analyses to address the following questions: *does community composition vary spatially? Are there direct effects of space on soil properties and stand age, and do these variables account for variation in community composition after the effects of space are removed? Is there residual spatial variation in community composition after accounting for soil properties and stand age?* In these analyses, we assumed that soil variables do not affect stand age and vice versa.

Prior to analysis we reduced the number of soil variables included in the analysis by omitting variables that were strongly correlated with one another (e.g. soil particle-size distributions, total cations, etc.). Because we selected this subset of variables prior to analyzing the data by forest type, our selection of variables was not biased by the effects of these variables on forest structure or composition. The final set of soil variables included: stone content, bulk density, %sand, %N, %K, %Mg, %P and %Zn. These variables include different aspects of soil physical properties, both a mono- and divalent cation, and the nutrients that best explain patterns of species richness among tropical forests, P and K (Clinebell et al., 1995). Soil variables were standardized to *Z*-scores prior to computing the distance matrix, to account for differing measurement units.

We computed three Euclidean distance matrices of all pairwise distances among plots for the soil variables, stand age and geographic distances. For community composition we used presence/absence data for all observed 135 species and trans-

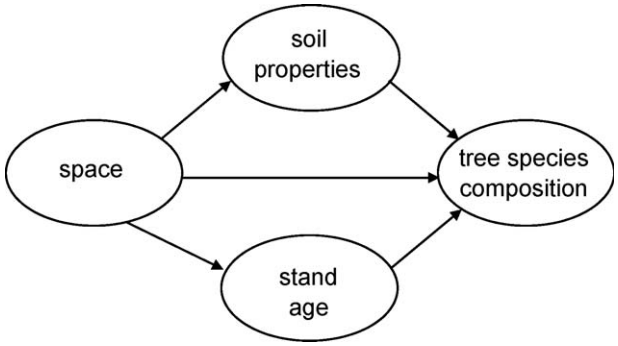

Fig. 2. Path diagram of hypothesized relationships among factors affecting species composition of secondary tropical dry forests.

formed these data into a Sorensen dissimilarity matrix prior to analysis. We assessed the significance of simple and partial Mantel correlations between distance matrices using one-sided *p*-values obtained from 10,000 randomizations (i.e. rows and columns of one matrix are randomized, the correlation is recalculated, and the procedure is repeated to build a random distribution to compare the test statistic against). The criterion for assessing the significance of Mantel correlation coefficients was adjusted for multiple comparisons by using a Bonferroni correction factor ($\alpha = 0.01$). If simple Mantel tests between space and soil properties or space and stand age were not statistically significant, we computed simple Mantel tests between these variables and species composition. In these cases we did not calculate partial Mantel tests because it was unnecessary to disentangle the co-variation between soils or stand age and species composition attributable to joint spatial autocorrelation.

3. Results

3.1. Edaphic characteristics

When data were averaged over age classes, there were large differences among forest types in surface soil physical characteristics (stone content, bulk density and particle-size distribution), total nutrient concentrations and pH (Table 1). Of the 19 variables we measured, 12 differed significantly (all significant differences refer to the Bonferroni-corrected criterion for assessing statistical significance) between SROAK and PVTDF, while only 7 differed significantly between SROAK and SRTDF and 6 differed significantly between PVTDF and SRTDF (Table 1). Soil chemical variables differed more among sites than soil physical properties. Mean soil pH was an entire unit lower in SROAK soils (pH 5.8) compared to PVTDF soils (pH 6.8), which was a highly statistically significant difference (Table 1). Concentrations of total nutrient cations including Ca, K, Mg, and Na differed among most of the forest cover types, and were always higher in PVTDF. Similarly, total soil P was 6 times higher in PVTDF soils compared to SROAK, with intermediate concentrations in SRTDF. Total organic C and N also followed these trends. Of the soil physical variables, bulk density (0–10 cm) was 4–12% higher in SRTDF compared to SROAK and PVTDF, respectively. While the stone content of SROAK soils was 3–4 times higher than in the other forest types, these differences were not statistically significant under the stringent Bonferroni correction factor we used, however, these are likely biologically meaningful differences.

Not surprisingly, soil properties were tightly correlated with one another. Of the 155 pairwise correlation coefficients calculated between soil properties, 108 were statistically significant at $\alpha = 0.05$ (Appendix A). The many statistically significant correlations among soil properties suggest that there are suites of soil chemical and physical characteristics that co-occur, and define a gradient from rocky, nutrient-poor soils (found in SROAK) to more clayey, nutrient-rich soils (PVTDF), with SRTDF soils intermediate between the two other forest types. The tight co-variation among soil variables also suggests that they are redundant to some extent, i.e. any one of these variables adequately captures the soil gradient, and thus our inferences regarding species' distributions across soil gradients should be robust to the choice of soil property.

Table 1
Soil chemical and physical properties (values are averages and SE across ages classes) for three different forest types of tropical dry forest in Costa Rica (number of plots sampled for different forest types is in parentheses). Within a row, forest types that do not share a letter differ significantly from one another at the Bonferroni-corrected $\alpha = 0.0009$.

Variable	SROAK ($N = 16$)	SRTDF ($N = 25$)	PVTDF ($N = 19$)
Bulk density ($g\ cm^{-3}$)	0.87 (0.05) ab	0.90 (0.02) a	0.77 (0.03) b
pH in water	5.82 (0.05) a	6.24 (0.06) b	6.83 (0.09) c
Sand (%)	38.94 (2.29) a	40.46 (1.11) a	40.12 (1.77) a
Silt (%)	34.66 (1.77) a	29.26 (1.39) ab	27.03 (0.65) b
Clay (%)	26.40 (1.74) a	30.27 (0.63) a	32.85 (1.68) a
Stone content ($g\ cm^{-3}$)	0.08 (0.02) a	0.02 (0) a	0.03 (0.01) a
C%	2.65 (0.26) a	3.79 (0.12) b	4.30 (0.25) c
N%	0.22 (0.02) a	0.35 (0.01) b	0.44 (0.02) b
B ($mg\ kg^{-1}$)	16.11 (0.56) a	20.90 (1.03) b	23.47 (1.41) b
Ca ($mg\ kg^{-1}$)	3622 (426) a	7520 (701) b	21516 (1310) c
Cr ($mg\ kg^{-1}$)	9.07 (0.52) a	12.95 (2.78) ab	61.93 (12.63) b
Cu ($mg\ kg^{-1}$)	44.37 (2.84) a	56.76 (2.87) a	79.83 (9.89) a
K ($mg\ kg^{-1}$)	540 (28) a	1244 (196) ab	1876 (233) b
Mg ($mg\ kg^{-1}$)	1163 (65) a	2309 (484) a	7872 (1147) b
Mn ($mg\ kg^{-1}$)	747 (102) a	789 (72) a	736 (56) a
Na ($mg\ kg^{-1}$)	567 (75) a	663 (42) a	1706 (149) b
Ni ($mg\ kg^{-1}$)	19.80 (8.66) a	12.57 (2.5) a	43.34 (7.68) a
P ($mg\ kg^{-1}$)	84 (15) a	358 (66) b	527 (55) b
Zn ($mg\ kg^{-1}$)	36.34 (2.72) a	53.16 (2.65) b	65.48 (3.86) b

In general, the stable isotopic composition of soil organic C, $\delta^{13}C$, corroborated the plot age estimates obtained from satellite image analysis and local, expert knowledge (Electronic Supplemental Appendix B). Soils of younger stands were more enriched with ^{13}C, reflecting a greater contribution of pasture grass-derived carbon to the soil organic matter, whereas older stands had $\delta^{13}C$ values more indicative of forest vegetation, consistent with longer periods of dominance by C3 trees.

3.2. Forest structure

In all plots, the density of woody vegetation (defined as number of stems ha^{-1}) decreased with increasing size class from seedlings > saplings > trees (10–30 cm DBH) > trees (>30 cm DBH) (Fig. 3), following classic "reverse J" patterns of tree recruitment (McLaren et al., 2005). The densities of seedlings, saplings and trees 10–30 cm DBH varied greatly among stands <40 years old, but declined with stand age in SRTDF and PVTDF (Fig. 3a–c) (R^2 values for best fit lines ranged from 0.12 to 0.52). In contrast, densities in these size classes increased with stand age in SROAK stands (although we caution that the age classes for SROAKS do not extend as long as for the other forest types, thus it is possible that this pattern may change with time). In all forest cover types, density of stems >30 cm DBH increased asymptotically with stand age from 0 to ~150 stems ha^{-1} (with R^2 values ranging from 0.42 to 0.61) (Fig. 3d).

3.3. Community composition and diversity

Across all forests, we measured 2260 trees >10 cm DBH and identified 135 species from 45 families (26 species were

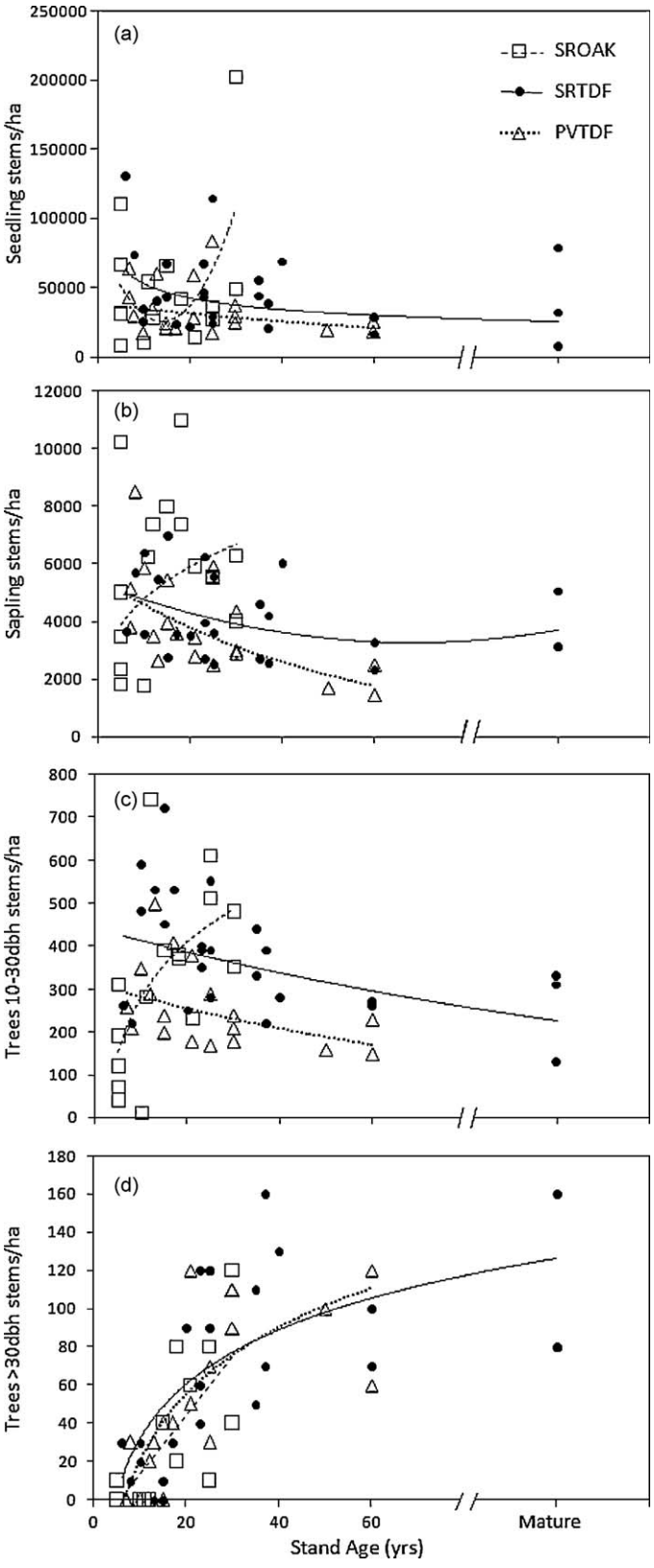

Fig. 3. Indices of forest structural attributes plotted as a function of stand age for three different forest types in Northwestern Costa Rica. Panels include (a) seedlings (i.e. woody plants <1.3 m height), (b) saplings >1.3 m height but <10 cm DBH, (c) trees 10–30 cm DBH, and (d) trees >30 cm DBH. Lines are best fit functions for each forest cover type abbreviated as follows: SROAK is oak forest at Sector Santa Rosa (SROAK), tropical dry forest at Sector Santa Rosa (SRTDF), and tropical dry forest at Palo Verde National Park (PVTDF).

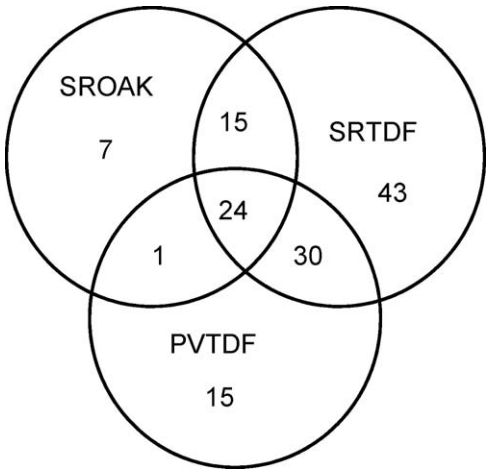

Fig. 4. Venn diagram depicting unique and shared species in plots of different forest ages in three vegetation communities, oak forest at Sector Santa Rosa (SROAK), tropical dry forest at Sector Santa Rosa (SRTDF), and tropical dry forest at Palo Verde National Park (PVTDF).

represented by only one individual) (Appendix C). Of these species, 24 were common to all forest types (Fig. 4), while SROAK had 7 unique species, SRTDF had 43 unique species, and PVTDF had 15. The higher number of unique species in SRTDF is certainly affected by the higher number of stems sampled in SRTDF (1113 compared to 554 for SROAK and 593 for PVTDF). Species accumulation curves provide a way to account for unequal sampling efforts; although our estimated species accumulation curves do not reach an asymptote (suggesting that these curves should be interpreted with caution because we did not encounter the entire species pool), they clearly suggest that SRTDF has higher species richness than the other forest types (Fig. 5).

The densities (estimated stems ha^{-1}) of the most abundant five species grouped by stand age classes reveal distinct patterns of species turnover within forest types as succession proceeds (Table 2). There was little turnover among the dominant species in the Santa Rosa oak forest across stand age classes (Table 2). Not surprisingly, *Q. oleoides* was the most abundant species, but both *Rehdera trinervis* and *Cochlosperum vitifolium* also appeared in the top five most abundant species in stands ranging from 5 to 30 years. In contrast, in SRTDF there was more turnover in the most abundant species among age classes. Both *R. trinervis* and *Gliricidia sepium* appeared in the most abundant five species during the first

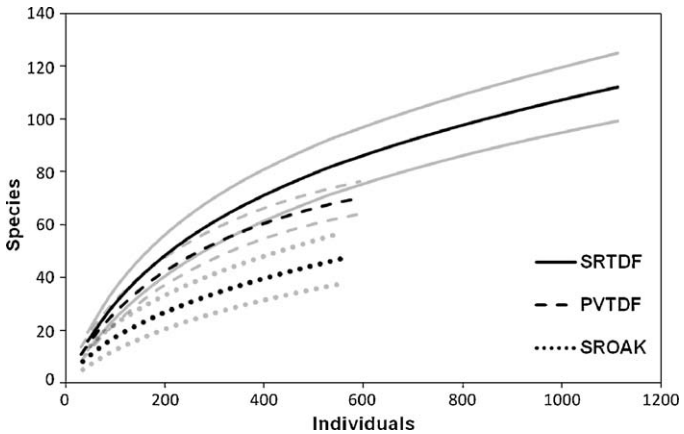

Fig. 5. Species accumulation curves averaged over stand ages for three forest types in Northwest Costa Rica, 95% confidence intervals in grey lines.

Table 2
Five most abundant species (pooled across plots within age classes) of trees > 10 cm DBH by forest type and age class in Costa Rica dry forests, and dispersal agent.

Forest type	Age class (number of plots in parentheses)	Top five most abundant species (stems ha^{-1})	Dispersal agent*
SROAK	<10 (6)	*Quercus oleoides* (57)	Animal (mammal)
		Rehdera trinervis (48)	Wind
		Byrsonima crassifolia (10)	Animal (bird, small mammal)
		Cochlospermum vitifolium (7)	Wind
		Dalbergia retusa (2)	Wind
	11–20 (5)	*Quercus oleoides* (230)	Animal (mammal)
		Rehdera trinervis (94)	Wind
		Cochlospermum vitifolium (30)	Wind
		Bursera tomentosa (24)	Animal (bird)
		Luehea speciosa (14)	Wind
	21–30 (5)	*Quercus oleoides* (104)	Animal (mammal)
		Cochlospermum vitifolium (74)	Wind
		Rehdera trinervis (60)	Wind
		Luehea speciosa (30)	Wind
		Ardisia revoluta (30)	Animal (bird)
SRTDF	<10 (4)	*Rehdera trinervis* (213)	Wind
		Semialarium mexicanum (28)	Wind
		Gliricidia sepium (23)	Explosive, dehiscent
		Machaerium biovulatum (23)	Wind
		Ateleia herbert-smithii (15)	Wind
	11–20 (5)	*Rehdera trinervis* (98)	Wind
		Gliricidia sepium (92)	Explosive, dehiscent
		Cochlospermum vitifolium (54)	Wind
		Lonchocarpus minimiflorus (44)	Wind
		Luehea speciosa (32)	Wind
	21–30 (6)	*Calycophyllum candidissimum* (65)	Wind
		Semialarium mexicanum (47)	Wind
		Bursera simaruba (42)	Presumably bird
		Sebastiania pavoniana (42)	Drop/wind
		Luehea speciosa (30)	Wind
	31–40 (5)	*Lonchocarpus parviflorus* (28)	Wind
		Manilkara chicle (24)	Animal (large bird, mammal)
		Trichilia martiana (24)	Animal (bird)
		Exostema mexicanum (22)	Animal (bird)
		Lonchocarpus minimiflorus (22)	Wind
	>40 (5)	*Manilkara chicle* (20)	Animal (large bird, mammal)
		Luehea speciosa (20)	wind
		Brosimum alicastrum (20)	Animal (birds, mammals)
		Gliricidia sepium (16)	Explosive, dehiscent
		Calycophyllum candidissimum (14)	Wind
PVTDF	<10 (4)	*Rehdera trinervis* (38)	Wind
		Tabebuia ochracea (38)	Wind
		Guazuma ulmifolia (23)	Animal (deer, cattle)
		Luehea speciosa (23)	Wind
		Lysiloma divaricatum (23)	Wind
	11–20 (5)	*Guazuma ulmifolia* (136)	Animal (deer, cattle)
		Cecropia peltata (24)	Animal (bats, birds)
		Tabebuia ochracea (20)	Wind
		Cordia collococca (16)	Wind
		Maclura tinctoria (14)	Animal (birds and other)
	21–30 (7)	*Guazuma ulmifolia* (71)	Animal (deer, cattle)
		Spondias mombin (47)	Animal (large birds, deer)
		Caesalpinia eriostachys (24)	Explosion/drop
		Tabebuia ochracea (21)	Wind
		Luehea speciosa (20)	Wind
	>40 (3)	*Spondias mombin* (83)	Animal (large birds, deer)
		Guazuma ulmifolia (33)	Animal (deer, cattle)
		Trichilia martiana (23)	Animal (bird)
		Calycophyllum candidissimum (17)	Wind
		Sapranthus palanga (17)	Animal

* Dispersal agent information from Jeff Klemens.

20 years of succession, but stands in the 21–30 year old age class had only one dominant species in common with younger age classes (*Luehea speciosa*). Stands that were over 30 years old were also dominated by different mixes of abundant species compared to younger stands, and the patterns of dominance changed. The most abundant species in the first three age classes had densities that ranged from 213 to 65 stems ha^{-1} (for stands aged <10 years and 21–30 years, respectively), however, the densities of the most abundant species in stands over 31 years old were only 28 stems ha^{-1} or fewer. In Palo Verde forests, *R. trinervis* appeared as one of the most abundant species in the youngest age class, as it was in both SROAK and SRTDF. *Guazuma ulmifolia* was one of the most abundant species in PVTDF in all age classes, with densities that ranged from 33 to 136 stems ha^{-1}. In contrast to SRTDF, the

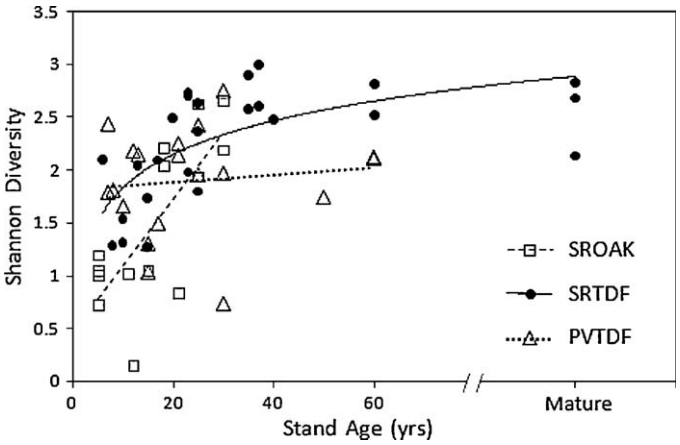

Fig. 6. Shannon diversity index (H′) as a function of stand age in plots of three types of tropical dry forest in Costa Rica.

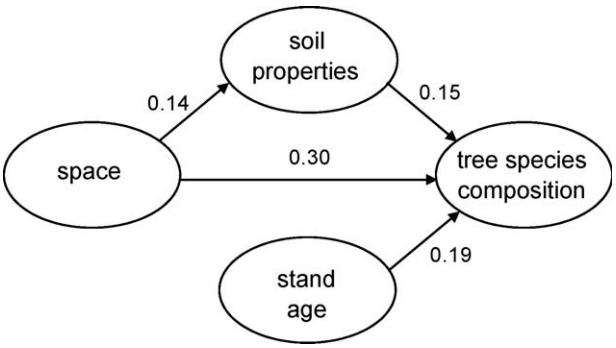

Fig. 7. Significant ($p < 0.01$) Mantel and partial Mantel correlation coefficients showing relationships among space, stand age, soil properties and forest community composition for all plots in the region ($N = 60$). Paths between "space and soils", "space and species" and "stand age and species" are simple Mantel tests. The path between soils and species shows the partial Mantel correlation given the common spatial patterns in both.

dominance of species composition by one or two species at PVTDF did not decrease in older stands, such that in plots over >40 years old, the most abundant species, *Spondias mombin* still comprised 83 stems ha^{-1}.

The Shannon diversity index (H′), which incorporates both richness and evenness of all species observed in the plots, provides another way to evaluate changes in community composition through successional time (Fig. 6). In SRTDF, diversity increases asymptotically from ~1.25 to 2.5 after about 50 years. In the oak forests, diversity is very low (~0.5) in young stands and increases linearly with stand age (note that we could not find oak stands >40 years old). In contrast, young plots at Palo Verde had higher initial values of diversity than the other forest types (~1.75), which remained relatively constant across stand age (Fig. 6).

3.4. Mantel path analysis of forest composition

Across all plots, simple Mantel tests between space (i.e. geographic distance) and soil properties, stand age or species composition revealed strong spatial structuring of soil properties and species composition, but not stand age (Fig. 7, Table 3). Because there was no statistically significant autocorrelation between space and stand age, we computed the simple Mantel correlation between stand age and species composition (Table 3). After controlling for the effects of space using partial Mantel test correlations, both soil properties (partial Mantel) and stand age (simple Mantel) explained a substantial portion of the variation in species presence or absence among plots, but stand age had a higher correlation coefficient than did soil properties. Last, after accounting for spatial variation in species composition that was not related to spatial variation in soils, there was still a strong, unexplained spatial component to the variation in forest composition with a correlation coefficient of 0.29 ($p = 0.0001$) (Table 3). In other words, plots that are closer together are more similar in species composition to one another than they are to distant plots, irrespective of stand age and soil properties (or the spatial co-variation of soils).

To see if this large amount of unexplained spatial variation in forest composition was related to β-diversity, i.e. regional turnover in species distributions among habitats, we reran the Mantel tests for each forest type separately (Table 3). At local scales within all forest types, soil properties still showed spatial autocorrelation, but the correlations were weaker than at the regional scale and none were significant at $\alpha = 0.01$. Similar to the regional analysis, stand age did not vary spatially in any forest type. Because neither soils nor stand age showed significant spatial autocorrelation at the local scales, we computed simple Mantel correlations between species composition and soil properties, stand age, and space (Table 3). Simple Mantel tests showed that stand age had a strong effect on tree species composition in both the Santa Rosa oak and tropical dry forest, but not at Palo Verde. Variation in soil properties was not correlated with variation in species composition at the local scale for any forest type. Finally, only in the SRTDF stands did forest composition vary spatially.

Table 3
Simple Mantel correlation coefficients (one-sided *p*-values in parentheses) for associations between soil properties, stand age or species composition and space (i.e. tests of spatial autocorrelation) and partial Mantel correlations testing for associations between species composition and soil properties or stand age, holding the effects of space constant, or residual spatial variation in species composition not explained by spatial co-variation between predictor variables. If simple correlations between predictor variables (soils, stand age) and space were not significant, simple Mantel correlations between these variables and species composition were calculated, but partial Mantel correlations were not.

	All plots	SROAK	SRTDF	PVTDF
Simple Mantel test				
Soil properties by space	0.14 (0.01)	0.17 (0.04)	0.26 (0.03)	0.28 (0.02)
Stand age by space	−0.05 (0.80)	−0.11 (0.94)	0.13 (0.14)	0.07 (0.24)
Species by age	0.19 (0.0014)	0.41 (0.0008)	0.31 (0.005)	−0.003 (0.48)
Species by soil	NA	0.21 (0.06)	0.21 (0.03)	0.12 (0.14)
Species by space	0.30 (0.0001)	0.05 (0.26)	0.28 (0.003)	0.16 (0.07)
Partial Mantel tests				
Species composition by soil/space	0.15 (0.003)	NA	NA	NA
Species composition by age/space	NA	NA	NA	NA
Species composition by space/soil	0.29 (0.0001)	NA	NA	NA

4. Discussion

Our study of how of forest structure and tree species composition vary in relation to stand age, soil properties and geographic distance across the extent of the Costa Rican dry tropical forest biome revealed many interesting patterns. Our key findings are that: (i) at a regional scale, patterns of β-diversity of Costa Rican TDF (i.e. turnover in species distributions across environmental gradients) are clearly correlated with soil properties, (ii) successional changes in forest structure differ by forest cover type, but in general forest structure recovered quickly, (iii) Shannon diversity recovers within about 40 years post-disturbance, but composition does not, and (iv) despite strong evidence for distinct forest types that are specialized to local edaphic conditions, stand age in general is a better correlate of species composition than soil properties within forest types. We discuss each of these points below, and conclude by speculating on the implications of these results for conservation and management of dry tropical forests in Costa Rica.

4.1. Forest cover types within Costa Rican tropical dry forest strongly co-vary with soil properties

The question of which factors affect species distributions within (α-diversity) and among (β-diversity) tropical forests has intrigued biologists for centuries (Wallace, 1889; Givnish, 1999). Across lowland Neotropical forests, species richness generally increases with mean annual precipitation (Gentry, 1988; Clinebell et al., 1995). In dry Neotropical forests in Mexico, a different climatic index, potential evapotranspiration, is the best correlate of species richness (Trejo and Dirzo, 2002). Within TDF, α-diversity may be maintained by species partitioning (i.e. sorting across) gradients of light, topography, or soil moisture (Segura et al., 2003; Vargas-Rodriguez et al., 2005).

In our study area, across a modest precipitation gradient we found large differences in soil characteristics that were well correlated with forest community composition. The large variation in soils undoubtedly reflects differences in geologic parent materials, geomorphic processes and soil age (Hartshorn, 1983), but what plants actually respond to, however, is how soil characteristics affect nutrient and water availability. The higher clay concentration, lower bulk density, and lower stone content of the Palo Verde soils suggest that these soils may have higher soil moisture than Santa Rosa TDF or oak forest soils (Powers, unpublished data). In addition to soil physical properties that affect water availability, total concentrations of major and minor plant nutrients range from 1 to 6 times higher at Palo Verde compared to Santa Rosa soils. In wet Neotropical forests, many studies have found that at local- to mesoscales (e.g. 50–800 ha), up to half of the tree species present have distributions that are related to soil nutrient availability (Clark et al., 1998; John et al., 2007). It is equally likely that dry forest tree species also segregating along nutrient and/or moisture gradients.

Gentry (1988) suggested that within a climatic zone, species richness is higher on soils of higher fertility, while others have suggested that highest species richness should be found on soils of intermediate fertility (reviewed in Givnish, 1999). We found highest species richness in the Santa Rosa tropical dry forest, a pattern that others have noted (Gillespie et al., 2000), which has soil properties that are intermediate to the Santa Rosa oak and Palo Verde forests (Table 1). The lowest species richness was on the poorest soils. While other studies have documented the localization of oak forest at Santa Rosa to thin pumice-derived soils (Boucher, 1983), ours is the first study to present quantitative data on how these soils vary from one another and also suggests a number of other species co-occur with *Q. oleoides* (Fig. 4). A number of these species are evergreen or semi-deciduous (e.g. *Q. oleoides*, *Ardisia revoluta*, *Byrsonima crassifolia*, and *Curatella americana*), a syndrome consistent with their dominance on poorer soils (Monk, 1966). Equally as interesting as the number of distinct species within each forest type is the large number of species shared between SR and PV tropical dry forests. Ongoing studies have been established to determine whether these large gradients in nutrient availability affect plant and ecosystem processes.

In summary, we found strong associations between soils and species composition at the regional, but not local scale, suggesting that changes in β-diversity among forest types was responsible for some of the residual spatial variation in regional community composition that was not explained by soil properties or stand age (Fig. 7, Table 3). In other words, for whatever reasons, e.g. dispersal limitation, historical factors or niche specialization to different soil conditions, each forest type we sampled has a different species pool, but within each soil/forest type associations between species composition and soil gradients were weak. Land-use history, i.e. the duration and intensity of previous grazing and/or cropping, is another potential, unmeasured factor that might explain variability in species composition aside from forest age (Uhl et al., 1988). From the standpoint of evaluating patterns of secondary succession, our data indicate different regeneration processes may be operating in each forest type.

4.2. Stand structural attributes recover within several decades, depending on forest type

In regenerating tropical wet and dry forests, indices of stand structure such as stem density, biomass, and basal area generally recover faster than community composition, often resembling those of old growth forests within 2–5 decades (Brown and Lugo, 1990; Aide et al., 2000; Kennard, 2002; Read and Lawrence, 2003; Kalacska et al., 2004; Marín-Spiotta et al., 2007; Ruiz et al., 2005). In our study, the densities of woody plants recruiting into different sizes classes <30 cm DBH decreased with increasing stand age for SR and PV tropical dry forest, and stand structure of regenerating forests appeared similar to mature sites after 40–60 years (Fig. 3a–c). As many other studies have shown, the density of larger individuals >30 cm DBH increased asymptotically with age (Fig. 3d), implying that in the older stands, mortality reduces the densities of younger (and smaller) trees, as more trees grow into larger size classes (Peet and Christensen, 1980).

In contrast to SRTDF and PVTDF, in the SROAK forests, stem densities in all size classes increased with stand age. One possible explanation for these patterns is that species traits such as dispersal mode account for the different regeneration dynamics among forest types. *Q. oleoides* stands out among many of the other species identified in our plots in that it has large, animal-dispersed seeds and forms associations with ectomycorrhizae (Klemens et al., 2008). Although *Q. oleoides* may resprout, most of the oak regeneration at Santa Rosa appears to be from seed (Klemens et al., 2008). Recent studies suggest that colonization of abandoned pastures in Santa Rosa by *Q. oleoides* is limited by the behavior of its main dispersal agent, the Central American Agouti (*Dasyprotca punctata*), who will traverse pastures but not cache seeds in them (Hallwachs, 1994; Klemens et al., 2008). Thus, one potential explanation for the pattern that we observed is that stem densities in SROAK increase with stand age in all size classes because patches of oak forest may be spreading outward by recruitment from a few isolated remnant trees in old pastures, which can produce copious seed crops (Klemens, personal communication), and self-thinning has not had sufficient time to occur. In other words, oak forest structure may change through successional time,

but these changes may not be revealed yet in the young stand ages of secondary oak forests that we sampled at Santa Rosa.

Despite the fact that our species-rich, tropical dry forest stands in both Palo Verde and Santa Rosa have complex disturbance histories, stand structural attributes across successional ages appeared very similar. In more species-rich forest types (i.e. not oak stands), the structure of regenerating secondary forests and characteristics such as balance between wind- versus animal-dispersed trees and evergreen versus deciduous species may depend on the landscape context of the sites and factors such as distance to seed sources, size of abandoned pastures, and the presence of fencerows or remnant trees that serve as foci for bird-dispersed seeds (Janzen, 1988a). The most abundant tree species (>10 cm DBH) in young stands at both Santa Rosa and Palo Verde, *R. trinervis*, is wind dispersed, as are other species that dominate early succession at these sites (Table 2). Moreover, although seedling growth of individual species can be limited by nutrient availability (Lawrence, 2003), it is interesting to note that at the plot level we observed no apparent differences in the rate of change in indices of forest structure on the more nutrient-rich soils at Palo Verde compared to SRTDF (Fig. 4).

4.3. Diversity and compositional changes through succession depend on forest type

Studies investigating secondary succession in wet tropical forests typically find that species diversity or species richness return to pre-disturbance or mature forest levels within several decades following abandonment, but species composition (i.e. the exact identities of those species) may require centuries to resemble mature forest (Chazdon, 2003). Our study suggests that successional changes in both tree species diversity and community composition vary with forest type within Costa Rican dry forests (Fig. 6, Table 2).

Two separate, independent analyses of our data show unexpected patterns of diversity in stands of different ages at Palo Verde. First, the Shannon diversity index varied little with stand age (Fig. 6). These data are consistent with the Mantel results of no effect of stand age on species composition (Table 3). Other studies of species composition and abundance at Palo Verde also have found flat patterns of Shannon diversity over stands with ages from 6 to 24 years (Hernández-Salas et al., 2002). There could be several explanations for this pattern in our data. First, at Palo Verde we may have sampled over distinct forest cover types, thus averaging over variation in different plant communities. The simple Mantel correlation of species composition by space (0.16, $p = 0.07$), was not significant at a Bonferroni-corrected p-value of 0.01, but provides suggestive, though weak evidence for this (Table 3). Further sampling is required to substantiate this, although we do point out that our study is one of the most extensive studies of forest composition in this are to date. Second, our oldest sites at Palo Verde predate the establishment of the park by several decades, and it is likely that these sites have been selectively harvested, grazed, or burned or affected by humans in other ways (Jiménez et al., 2001). The conspicuous prevalence of *G. ulmifolia* at Palo Verde in all age classes (González, 2002; Hernández-Salas et al., 2002), which has hard, round fruits dispersed by cows (Table 2), may be a legacy of the use of grazing as a management tool to reduce fuel loads of *H. rufa* (Janzen, 1982). Other studies at Palo Verde corroborate this interpretation. Stern et al. (2002) compared tree diversity in plots at Palo Verde subjected to intermittent cattle grazing with plots of the same age that were not grazed. Species richness was lower and dominance by *G. ulmifolia* was higher in the grazed plots, and these authors conclude that grazing is an ineffective tool for facilitating dry forest restoration (Stern et al., 2002).

In both forest types at Santa Rosa, Shannon diversity increased with stand age (although the form of that relationship differed between oak forest and TDF), and stand age was the best correlate of community composition (Table 3). The finding that stand age was a better predictor of community composition than local soil properties or geographic distance suggests predictable patterns of species turnover through secondary succession. Janzen (1988a) proposed that the phases of early colonization of abandoned pastures occur along two trajectories and become dominated by wind-dispersed or animal-dispersed species. Stands regenerating from wind-dispersed seeds can maintain that species composition for a long time (decades to centuries) in somewhat of a positive feedback; wind-dispersed seeds arrive first and those species grow, they provide little incentive for animals to colonize this type of forest (given that there are not attractive food resources for animals), and that reinforces a wind-dispersed community. Similarly, patches of regenerating forest expanding outward from animal-dispersed "nuclear" tree species in pastures, fence rows, or edges of older forests may initially be colonized by animal-dispersed species, and these species remain dominant for decades to centuries. Our data provide mixed evidence for this hypothesis, and suggest that community composition may be more dynamic over the 60 years of succession in our dataset.

The oak forests likely regenerate by recruitment from remnant oaks in old pastures. We found other animal-dispersed trees such as *B. crassifolia* in the top five most abundant species in young oak forests (<10 years), and other animal-dispersed species besides *Q. oleoides* appeared as dominant species in stands 20–30 years old. In the stands between 0 and 20 years old in TDF (both SRTDF and PVTDF), the most abundant species are all wind dispersed or dehiscent (*G. sepium*), clearly indicating dispersal by wind as the most important pathway for seeds to arrive at the sites we sampled. If we assume that the older stands we sampled originated in a similar way as the younger stands, we see a different pattern of dominant dispersal modes by 20 years. Some species of bird-dispersed seeds become dominant after 20 years, and after 30 years many of the species that are most abundant in SRTDF are dispersed by birds.

4.4. Conclusions and implications for conservation and management

While the history of tropical dry forests has been one of exploitation by humans, the future of these unique and diverse ecosystems also depends on how people conserve, manage and restore them. We studied the patterns of secondary forest regeneration occurring in protected areas in Costa Rica. The two conservation areas have relied on preventing fires (either via reducing fuel loads from grazing or active fire control) as the main management tool to facilitate secondary forest regeneration, as opposed to more labor-demanding strategies such as enrichment plantings. Our results show that these have been successful strategies in terms of fostering an environment for regeneration to occur; both indices of forest structure and species richness approach levels of mature forest within 4–5 decades. However, if certain species composition is desired (i.e. trees with animal-dispersed seeds) more active restoration strategies may be needed. For example, our data suggest that the dynamics of secondary succession are different in the Santa Rosa oak forest, where vertebrate-dispersed species predominate, in comparison to the other forest types in the region where wind-dispersed tree species dominate early successional communities. Our data also suggest that fire control methods affect forest composition differentially, and that grazing in Palo Verde may contribute to the high dominance by *G. ulmifolia* in regenerating stands. Another management issue that our results highlight is the importance

of establishing multiple protected areas throughout the range of the tropical dry forest biome in order to conserve both α- and β-diversity. From our dataset in Costa Rican dry forest biome, β-diversity appears to be correlated with edaphic factors. Irrespective of the cause of this pattern, conservation efforts must appreciate that a conservation area established to conserve diversity in one location may not be sufficient to preserve all species in the larger region.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2008.10.036.

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