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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 $\times$ 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