Forest Ecology and Management 335 (2015) 270–280

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Land use legacy effects on structure and composition of subtropical dry forests in St. Croix, U.S. Virgin Islands

Emily E. Atkinson *, Erika Marín-Spiotta

Department of Geography, University of Wisconsin-Madison, 550 N. Park St., Madison, WI 53706, United States

ARTICLE INFO

Article history:
Received 8 July 2014
Received in revised form 24 September 2014
Accepted 27 September 2014
Available online 29 October 2014

Keywords:
Tropical dry forest
Secondary forest
Land change
Hurricane
N-fixing species
Novel ecosystem

ABSTRACT

Tropical dry forests are subject to intense human pressure and land change, including conversion to agricultural crops, pasture or agroforestry, and urban encroachment. Decades, and even centuries, of conversion, expansion, regrowth, and changing land-use practices can result in a mosaic of secondary growth patches with different land-use histories. Whereas post-agricultural landscapes may appear as contiguous areas of forest regeneration, the successional trajectory of forest patches from historic land cover to their current state may differ substantially, with consequences for species composition and ecosystem structure and function. We examined the effect of different land-use histories on current forest structure, biomass, and composition in subtropical dry forests in St. Croix, U.S. Virgin Islands. We sampled three types of secondary forests that followed different regeneration pathways after centuries of sugarcane agriculture: 40-year old secondary forests that naturally regenerated after sugarcane abandonment, 40-year old secondary forests that were reforested with timber plantations before management ceased and they were overtaken by natural succession, and 10-year old secondary forests that were intensive pasture prior to recent forest regeneration. Secondary forests that naturally regenerated after sugarcane had similar structural characteristics, in terms of basal area, stem density, aboveground biomass, and species diversity compared to secondary forests of the same age that were former plantations. Species composition, however, remained distinct. Compositional differences between the two types of 40-year old secondary forests could be partially attributed to plantation species, specifically *Swietenia mahagoni*, whereas naturally regenerated forests were dominated by common secondary forest species, such as *Melicoccus bijugatus* and *Cordia alba*. The effects of hurricane damage helped to explain structural similarity and compositional dissimilarity between naturally regenerated secondary forests and former plantations. Forest age had a significant effect on forest structure and composition. Differences between 10-year old and both types of 40-year old secondary forests were driven by a dominance of the nitrogen-fixing species *Leucaena leucocephala*, which rapidly established in 10-year old secondary forests and resulted in greater stem density and lower basal area, biomass, and species richness. Our results show that land-use history plays an important role in shaping species composition, especially in post-agricultural tropical dry forests. Although forests with differing land-use histories may structurally resemble one another within decades of abandonment, species composition may remain distinct for much longer. Understanding the legacy of human land use is important for dry forests that have a long history of disturbance and for predicting their response to future environmental change.

1. Introduction

Tropical dry forests are the most perturbed, heavily used, fragmented, and threatened tropical forests (Janzen, 1988; Miles et al., 2006; Quesada et al., 2009). Compared to all other biomes of the world, tropical dry forests have experienced the greatest habitat loss and land conversion due to increasing human population growth and have one of the lowest proportions of area under protection and conservation (Hoekstra et al., 2004; Janzen, 1988; Miles et al., 2006; Portillo-Quintero and Sánchez-Azofeifa, 2010). Subtropical and tropical dry forest life zones, characterized by strong seasonality in rainfall and several months of drought, occupy 42% of the global tropics (Brown and Lugo, 1990) and about 50% of land in Central America and the Caribbean (Murphy and Lugo, 1995). Nearly 80% of tropical land with mean annual rainfall ⩽ 1500 mm has experienced > 50% conversion from natural vegetation to human use (Powers et al., 2011).

---

* Corresponding author. Tel.: +1 608 262 1855.
E-mail address: eeatkinson@wisc.edu (E.E. Atkinson).

http://dx.doi.org/10.1016/j.foreco.2014.09.033
0378-1127/© 2014 Elsevier B.V. All rights reserved.

Caribbean dry forests are the least conserved (Molina Colón et al., 2011; Lugo et al., 2006) and have undergone significant deforestation due to colonial plantation economies and high densities of human population in lowland, coastal areas. After centuries of agricultural use, abandonment of plantation agriculture in many Caribbean islands has led to widespread secondary forest regeneration (Aide et al., 2012; Álvarez-Berríos et al., 2013). A prime example of extensive land change and subsequent shift to secondary forest is the Caribbean island of St. Croix, U.S. Virgin Islands. Prior to Danish colonization in 1733, the U.S. Virgin Islands had 90% forest cover (Brandeis and Oswalt, 2007; The Nature Conservancy, 2003; Haagensen, 1995). Following colonization, more than half (54%) of the island of St. Croix was converted to sugarcane agriculture, particularly in the flat central lowlands. Sugarcane cultivation lasted there for over 200 years until the early 20th century, with some areas continuing in production until the mid-1950s (Weaver, 2006). The decline of the sugarcane industry led to island-wide pasture establishment and agroforestry development. By 1917, an estimated 90% of St. Croix had been cleared for agriculture and logged for valuable timber (Ward et al., 2000). During the mid- to late-20th century much of the intensive pasture and agroforestry activities ceased. Whereas there are currently some parts of the island in active pasture, post-agricultural forests now cover approximately 50% of land on St. Croix (Brandeis et al., 2009; Brandeis and Oswalt, 2007). This secondary forest cover is predominantly composed of relatively young forests with only 3% in mature forest stands (Brandeis and Oswalt, 2007). Early successional forests consist of mostly small diameter trees and reflect centuries of past and recent land use.

The result of this dynamic history has been a mosaic of secondary forests that have followed different pathways to their current state – some secondary forests regenerated almost immediately after sugarcane abandonment, while others only recently regenerated after extensive pasture or agroforestry use. The objective of our study was to examine whether differences in land-use history led to differences in forest structure, aboveground biomass, composition, and species diversity in subtropical dry forests. Our approach was to measure the effect of land-use history and successional trajectories by controlling for climate and soil type. Thus, we compared common post-agricultural secondary forest types found in St. Croix, including naturally regenerated secondary forests, former timber plantations, and younger recently regenerated secondary forests.

2. Methods

2.1. Site description

We conducted this research in subtropical dry forests of St. Croix, U.S. Virgin Islands (17°44′N, 64°43′W). Three replicate post-sugarcane secondary forest types were identified with the following land-use histories: (1) cessation of sugarcane followed by a short period of low intensity pasture use (7–20 years) and 40 years of natural forest regeneration, hereafter referred to as 40-year old secondary forests; (2) cessation of sugarcane followed by low intensity pasture use and managed reforestation with timber plantations, which are no longer being managed and have regenerated to secondary forests, hereafter referred to as 40-year old former plantations; and (3) cessation of sugarcane followed by a long period of high intensity pasture use (30 years) and recent natural forest regeneration, hereafter referred to as 10-year old secondary forests (Table 1). The former timber plantation sites were experimental sites that had been planted with mahogany (*Swietenia mahagoni*), teak (*Tectona grandis*) or mastic (*Sideroxylon foetidissimum*). The first two were part of the USDA Estate Thomas Experimental Forest, where planting occurred during 1954–1972 (Weaver, 2006). Early measurements from Estate Thomas showed that some of the densest stands, mostly *S. mahagoni*, had basal areas of 45 m^2/ha (Wadsworth, 1947). The third plantation site was privately owned property adjacent to the University of the Virgin Islands. While management practices at the three former plantation sites differed, they were all planted, harvested, and then abandoned at comparable times. Harvesting began in 1963 and continued regularly until abandonment (Weaver, 2006). All sites were identified by reconstructing land-use history through the use of documented land-use history records, archived maps, and personal communication with local farmers, government officials, landowners, and researchers affiliated with the University of the Virgin Islands and the Virgin Islands Department of Agriculture.

All sites were located in the subtropical dry life zone (Fig. 1). Mean annual precipitation at sites was approximately 1060 mm with a mean annual temperature of 26.4 °C (1971–2001 from climatic stations located in Christiansted Fort and Bethlehem Upper New Works) (Weaver, 2006). Sites were chosen in order to control for parent material, soil order and slope. Soils at all sites are classified as Mollisols and are part of either the Sion soil series, consisting of shallow, well-drained, slowly permeable soils formed in material weathered from soft limestone bedrock (*Typic Haplustolls*) or the Arawak soil series, consisting of very deep, well-drained, moderately slowly permeable soils formed in alkaline marine deposits (*isohyperthermic Typic Calciustolls*) (Soil Survey NRCS). All sites were located on flat topography at 9–127 m above sea level.

2.2. Forest structure and composition

Sites were sampled during January and June 2013. At each site, we established four 1 × 25 m parallel transects to measure and identify all live, rooted trees with diameter at breast height (dbh) <10 cm and $\geqslant 1$ cm and stem length of at least 1.3 m (Fig. 2), following the methods of Aide et al. (2000). The trees in this size class will hereafter be referred to as "small" trees. Two 8 × 25 m parallel transects were overlain on top of the small tree transects to measure dbh for all trees $\geqslant 10$ cm and stem length of at least 1.3 m, hereafter referred to as "large" trees (Fig. 2). All multiple stems from a single base that satisfied the dbh and height requirements were measured. Trees were identified to the species level according to Little and Wadsworth (1964, 1974) and with assistance from researchers at the University of the Virgin Islands and the director of the St. George Village Botanical Garden. Voucher specimens were collected and deposited at the St. George Village Botanical Garden in St. Croix.

For each site, stems and basal area were summed for the small tree (total of 100 m^2) and large tree (total of 400 m^2) transects. Basal area (m^2/ha) and stem density (n stems/ha) were calculated for all small and large stems. Importance values (IV) were calculated as the sum of relative stem abundance and relative basal area per site for each species (Marín-Spiotta et al., 2007). For each tree species, IV ranged from 0 (no species present at site) to 2 (site is comprised entirely of a single species).

2.3. Diversity and dissimilarity

Shannon-Weiner diversity (H') and evenness (E_H) were calculated for individuals:

$$H' = -\sum_{i=1}^{R} p_i \ln p_i \tag{1}$$

$$E_H = H'/\ln S \tag{2}$$