Forest Ecology and Management 349 (2015) 4–11

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Effects of soil conditions on the diversity of tropical forests across a successional gradient

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ARTICLE INFO

Article history:
Received 1 November 2014
Received in revised form 16 April 2015
Accepted 18 April 2015
Available online 30 April 2015

Keywords:
Atlantic forest
Brazil
Succession
Resilience
Tropical soil

ABSTRACT

Soil features are an important factor influencing plant growth and distribution in different parts of the tropics. We hypothesized that in forests recovering from a disturbance, the spatial and temporal variation of soil proprieties could determine differences in forest structure and composition. We addressed this question by comparatively assessing the soil traits and forest structure and diversity that occur in two contrasting soils in second growth tropical forests of southern Brazil: Cambisols (well-drained and nutrient-poor soil) and Gleisols (periodically flooded and with greater soil Al toxicity). Three replicates of four combinations of four forest ages (9–11, 15–20, 40–55, and >100 years since abandonment) and two soil types (Cambisol and Gleisol) were compared, thus encompassing 21 plots that covered 2.1 ha. A total of 3355 individuals of 151 tree species were sampled in all plots. Soil characteristics changed along the succession, with Al toxicity increasing as the forests aged. Cambisols and Gleisols differed in their nutritional and structural characteristics. Forests growing in both soil types exhibited higher species density, individual density and basal area along the successional gradient, but diversity (and evenness) was higher in forests growing in Gleisol soils. Moreover, soil characteristics (sand:clay, C:N, and Al and P concentrations) and forest age determined the differences in community assemblies among soils. Considering that soil characteristics are spatially and temporally variable in the tropics and that these variations are poorly measured in successional studies, we argue that small-scale variations in soil characteristics can potentially be a powerful factor influencing the successional trajectories of second growth tropical forests in tropical regions.

1. Introduction

Soil conditions are known to be important abiotic factors influencing plant distribution (Sollins, 1998; Swanson et al., 1988). In the tropics, the fixation of phosphorus and aluminum toxicity associated with nitrogen losses were some of the factors that plants inevitably had to overcome during their evolutionary development (Sollins, 1998). As a result, trees have developed different survival strategies, including the maintenance of nutrients in living biomass, the rapid incorporation of nutrients from dead matter, and tolerance mechanisms for excess aluminum, among others (Golley et al., 1975). In addition to these limitations, there is significant variation in the texture, nutritional status and water availability in tropical soils (Longman and Jeník, 1987), resulting in diverse adaptations that affect both the distribution patterns and the structure of plant communities (Jordan, 1985).

Soil texture, nutrient concentration and moisture levels strongly affect the growth of tropical trees in different ways. Soils with medium clay content (30–60%) tend to favor tree height and diameter growth. Additionally, higher levels of N, P, K and Ca are positively related to radial growth and phenology (Cardoso et al., 2012), to seedling height (Paul et al., 2010), and to plant biomass (Clark et al., 1998; Laurance et al., 1999; Castilho et al., 2006). Because the level of the water table is directly related to the degree of flooding, soils with a shallow water table limit root aeration, reducing tree growth (Schöngart et al., 2002). Therefore, it is expected that variations in soil characteristics play an important role in the dynamics of tropical forests.

A tropical forest is subjected to a number of dynamic processes following a disturbance that trigger an unpredictable and highly variable successional trajectory (Chazdon, 2008; Glenn-Lewin et al., 1992). This trajectory can be influenced by numerous factors, such as the type and intensity of disturbance (Hooper et al., 2004), as well as the distance of the propagules' sources (Kauano et al., 2013). As soil characteristics largely determine the distribution of

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http://dx.doi.org/10.1016/j.foreco.2015.04.018
0378-1127/

plants (Brady and Weil, 2002; Maestre et al., 2006; Webb, 1969), it is possible that the speed and direction of structural and floristic changes during succession may also be influenced by soil. Previous studies have linked variations in plant growth and survival with soil conditions in disturbed tropical areas (Ceccon et al., 2002; Ganade and Brown, 2002; González-Iturbide et al., 2002; Mizrahi et al., 1997), but none have explicitly tested a forest's successional development in contrasting soil conditions.

Less than 16% of the original cover of the Atlantic Forest – the most diverse of all Brazilian rainforest biomes that have been impacted by 500 years of colonization – remains intact (Ribeiro et al., 2009). In southern Brazil, approximately 30% of the forested areas (Kauano et al., 2012) have been cleared for cattle ranching and agriculture, which were the predominant industries in this region during the 1970s and 1980s (Ferretti and Britez, 2006). Although soils in southern Brazil are variable (including Ultisols, Inceptisols, and Entisols), they are generally incapable of supporting intensive cropland or pastureland use, leading farmers to abandon fields after 20–30 years of use. These shifts in land use have thus resulted in a mosaic of second growth forests that differ in soil conditions and forest age (Cheung et al., 2010; Liebsch et al., 2007).

The aim of the present study was to evaluate the structure and diversity of second growth forests that ranged in age following disturbance (9–11 years, 15–20 years, 40–55 years, and >100 years) and that occur in two different soil types (Gleisols and Cambisols) in southern Brazil, in an effort to verify whether soil characteristics can drive different forest structure and composition. We sought to determine (1) whether soil characteristics at different depths vary according to successional gradients and (2) whether forests of the same age but growing on different soil types differ in species composition and structure (species density, tree density and basal area).

2. Material and methods

2.1. Study site

The study was conducted in Rio Cachoeira Natural Reserve (25°18′51″S and 48°42′24″W), a protected area located in the municipality of Antonina, Paraná State, southern Brazil. The reserve covers an area of 8600 ha and has a Cfa climate according to the Köppen classification, defined as being subtropical humid mesothermal (Peel et al., 2007). Average annual temperature in the reserve ranges between 20 °C and 22 °C, average precipitation ranges between 2000 and 3000 mm, frosts are rare, and there is no dry season (Ferretti and Britez, 2006).

The reserve sits on gneisses and migmatites from the Precambrian, basic and intermediate dikes (Jurassic to Cretaceous), and Cenozoic sedimentary deposits (IPARDES, 2001). The local relief stretches from sea level to steep sections of land reaching 540 m in altitude. The vegetation in the region consists of the Atlantic Rain Forest and its sub-types: Lowland, Lower Montane, Montane and Alluvial Forests (Veloso et al., 1991). The ecosystems of the region were markedly disturbed in the late nineteenth and early twentieth century by agricultural activities and buffalo ranching (Ferretti and Britez, 2006). These activities were abandoned at different periods of time, and the forests recovered naturally, resulting in the current mosaic of connected successional forests.

2.2. Sampling design

We systematically chose areas with Cambisol and Gleisol soils in the Rio Cachoeira Natural Reserve where disturbance had ceased, resulting in the selection of forests of four different age categories: 9–11 years, 15–20 years, 40–55 years, and >100 years. The soil types were previously mapped in the reserve (Ferretti and Britez, 2006), and the forest age classification was created by superimposing aerial photographs from different time periods (1952, 1980 and 2002). Interviews with former residents confirmed the age classification. All areas (with the exception of areas >100 years old) experienced clear cutting, grazing and agricultural land use prior to abandonment and the beginning of forest regeneration. The older area within the Cambisol soil forest was subjected only to low-impact selective logging in the past. Each sample area thus consisted of a combination of soil type and age (in years) as follows: Cambisol 9–11 years, Cambisol 15–20 years, Cambisol 40–55 years, Cambisol >100 years, Gleisol 9–11 years, Gleisol 15–20 years, and Gleisol 40–55 years. Each combination was spatially distributed throughout the reserve, with each category consisting of three independently distributed replicates (~1000 m apart). Due to the absence of certain forest types, the experiment did not include Gleisol >100 years (thus, this soil type consisted of only three age groups). At each area described above, a 1000-m^2 (10 × 100 m) plot was established (for a total of 21 plots covering 2.1 ha) and divided into 10 sub-plots of 100 m^2 each. Thus, the sampling design included three independent factors: factor 1 (soil type, two levels), factor 2 (time after disturbance, four levels in Cambisol and three levels in Gleisol), and factor 3 (soil depth, three levels).

2.3. Soil characteristics, collection and analysis

The predominant soil type in each area was classified by visual inspection according to the Brazilian System of Soil Classification (EMBRAPA, 1999). Gleisols (Entisols). Soils are hydromorphic and permanently or periodically flooded, composed of mineral material and exhibit variable soil texture. The areas of Gleisols included in this study were 10 m above sea level and are strongly influenced by groundwater percolating to the surface during warmer and wetter periods of the year. These soils are shallow and do not exceed 40 cm in depth (Santos, 2007). Cambisols (Inceptisols) are composed of highly variable mineral material and vary greatly in drainage, depth and base saturation (EMBRAPA, 1999). The sampled areas of Cambisols were at least 260 m above sea level, are deep (60 cm in depth) and are not flooded (Santos, 2007).

Three soil samples from three depths (0–5 cm, 5–10 cm and 10–20 cm) were collected (samples of ~1.6 L) at each 1000-m^2 plot. These three depths are typically used in soil analysis because they represent chemical and textural characteristics that result from different processes during soil formation (Santos, 2007). We composed one unique sample representing the plot for each sample depth collected in each plot. The samples were analyzed in the laboratory following regular protocols (EMBRAPA, 1979). The determination of particle size followed EMBRAPA (1997). Carbon and nitrogen in samples were analyzed using a CNHS analyzer (Elementar model Vario El).

2.4. Vegetation survey

We sampled all trees with a diameter at breast height (DBH) ⩾ 4.8 cm in each of the 100-m^2 subplots and recorded both the species and DBH for each individual tree. Vouchers were determined by comparison with specimens from herbarium collections or by consulting plant taxonomists.

2.5. Data analysis

In our analysis, we considered factor 3 (soil depth, three levels) nested in factor 2 (time after disturbance, four levels in Cambisol and three levels in Gleisol) and factor 2 nested in factor 1 (soil type,