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## Research article

# Pathways, mechanisms and predictability of vegetation change during tropical dry forest succession

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## ABSTRACT

The development of forest succession theory has been based on studies in temperate and tropical wet forests. As rates and pathways of succession vary with the environment, advances in successional theory and study approaches are challenged by controversies derived from such variation and by the scarcity of studies in other ecosystems. During five years, we studied development pathways and dynamics in a chronosequence spanning from very early to late successional stages (ca. 1–60 years) in a tropical dry forest of Mexico. We (1) contrasted dynamic pathways of change in structure, diversity, and species composition with static, chronosequence-based trends, (2) examined how structure and successional dynamics of guilds of trees shape community change, and (3) assessed the predictability of succession in this system. Forest diversity and structure increased with time but tree density stabilized early in succession. Dynamic pathways matched chronosequence trends. Succession consisted of two tree-dominated phases characterized by the development and dynamics of a pioneer and a mature forest species guild, respectively. Pioneer species dominated early recruitment (until ca. 10 years after abandonment), and declined before slower growing mature-forest species became dominant or reached maximum development rates (after 40–45 years). Pioneers promoted their replacement early in succession, while mature-forest species recruited and grew constantly throughout the process, with their lowest mortality coinciding with the peak of pioneer abundance. In contrast to prevailing stochastic views, we observed an orderly, community driven series of changes in this dry forest secondary succession. Chronosequences thus represent a valuable approach for revealing system-specific successional pathways, formulating hypotheses on causes and mechanisms and, in combination with repeated sampling, evaluating the effects of vegetation dynamics in pathway variation.

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## Introduction

The study of secondary succession has exerted a major influence on developments in theoretical ecology and on the practice of vegetation restoration and management. Succession is affected by multiple interacting factors, both intrinsic (autogenic) and extrinsic (allogenic) to plant communities (Pickett et al., 1987). This implies that both ecosystem- and site-specific research on succession are fundamental to strengthen its theoretical basis (Pickett et al., 1987; Walker et al., 2007; Peterson and Carson, 2008), as shown by the rich debate on the relative importance of mechanisms that drive such complex process (Hooper et al., 2004;

Chazdon, 2008; Schiffrers et al., 2010). Present forest secondary succession theory derives mostly from studies in temperate and tropical humid ecosystems (Chazdon, 2008; Quesada et al., 2009), for which the diversity of successional pathways and mechanisms observed has resulted in a continuous refinement of successional models (MacMahon, 1981; McCook, 1994; Denslow and Guzman, 2000). However, the applicability of these models to other biomes is rarely addressed and not necessarily warranted (McCook, 1994; Peterson and Carson, 2008).

The large variability that characterizes secondary successions has promoted a shift in our thinking about succession. Following Clements' (1916) early view, succession was once considered to be essentially directional (i.e. niche-based, deterministic) and thus predictable, but now it is often seen as being highly idiosyncratic, contingent and mainly stochastic (Finegan, 1984; Vandermeer et al., 2004; Feldpausch et al., 2007; Chazdon, 2008), more in line with Gleason's (1926) conceptualization of the process. To evaluate

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the predictability of succession, one should consider the spatio-temporal scale of analysis (Cramer, 2007; Fraterrigo and Rusak, 2008). A major limitation for our understanding of forest succession is the short time usually available for its study, relative to the generally longer time span over which the process takes place (decades/centuries). Chronosequences (a set of sites with different ages since disturbance) have been used to circumvent such problem. Chronosequences allow to identify successional patterns and formulate causal hypotheses on its main driving forces (Foster and Tilman, 2000), but they do not inform on successional rates or mechanisms, a purpose for which long-term studies in permanent plots are required (Bakker et al., 1996). Moreover, either because many studies have not complied with chronosequence requirements (which is analogous to conducting an uncontrolled experiment), or because under certain circumstances successional development follows idiosyncratic trajectories (Vandermeer et al., 2004), the chronosequence method and its findings are frequently criticized (Miles, 1979; Walker and del Moral, 2003; Johnson and Miyanishi, 2008). Few appraisals of chronosequences are, however, based on contrasts of static and vegetation dynamics data. This is unfortunate because chronosequences are useful for a variety of subjects; for instance, productivity and nutrient cycling (Hughes et al., 1999; Feldpausch et al., 2004) or forest restoration and management (Quesada et al., 2009).

Studies of secondary succession in tropical dry forests (TDF) are scarce despite their large extent (>40% of forests) in tropical regions (Murphy and Lugo, 1986; Quesada et al., 2009). TDF are seasonally drought-stressed forests, with rainfall (500–2000 mm) strongly concentrated in a 4–7 months period. Accordingly, the TDF flora displays distinct adaptations to cope with drought and irradiance stresses (Medina, 1995; Holbrook et al., 1995; Lebrija-Trejos et al., 2010), and tends to be less diverse than the moist forest flora (Gentry, 1988). Also, TDF have a lower productivity and a more simple vertical structure, both of which shape distinct disturbance regimes and responses (e.g. Dickinson et al., 2001). Because of the harshness of the dry forest environment, facilitation is likely to play a key role during succession (Holmgren et al., 1997; Holl, 2007) and a convergence in community assembly is expected (Chase, 2007).

In this study we combined chronosequence and vegetation dynamics data to analyze patterns and causes of change during TDF succession. To our knowledge this is the first study to examine TDF succession using such combined approach, and one of the few ones in the tropics to do so from very early to late stages (Sheil, 1999, 2001). We asked: (1) how do structure, diversity, species composition and successional dynamics (i.e. recruitment, growth and mortality) of the community vary over time? (2) Do structure and successional dynamics of functional groups of trees shape community change and influence each other's development? And (3) how directional is vegetation development, i.e. can chronosequence trends predict individual temporal pathways? Given a low level of landscape fragmentation, similar site disturbance histories, and a homogeneous climate in the study region, we expected successional forests to show clear time-related structural changes and transitions between species groups. Therefore, the chronosequence-based successional model should reflect individual-site development pathways. We discuss our findings regarding the mechanistic bases of succession in relation to the studied TDF environment, and the controversy around successional predictability and chronosequence studies.

## Materials and methods

The study was conducted in Nizanda (16°39'30"N, 95°00'40"W), Oaxaca State, S Mexico. Annual rainfall in the area is ca. 900 mm and

is highly seasonal, with a strong dry season lasting 6–7 months (November to May); mean annual temperature is ca. 26°C. The regional vegetation cover is a mosaic of community types associated to different geological substrates, soils, and topographic conditions (Pérez-García et al., 2001, 2010). Areas devoted to shifting agriculture are uniquely located within a matrix comprising a mixture of old-growth, low-stature (7–10 m) TDF (Pérez-García and Meave, 2006) and secondary forests of different ages.

Sixteen 30 × 30 m successional sites (fallows) with time since abandonment (age) ranging from <1 year to ca. 60 years, and one mature forest site, were selected from field surveys conducted in 2003 (the two oldest fallows with ages between 55 and 60 years were added in 2005). For their long-term use, sites were fenced to mark their limits and discourage human entrance while permitting passage to browsers (Lebrija-Trejos et al., 2008). Site age was obtained from interviews with land-owners and verified through tree ring analyses (Brienen et al., 2009). All sites shared a single geological substrate (phyllite) and had similar topographic positions (mid-slope hillside or piedmont) and elevations. The fallows derive from traditional shifting cultivation, were burned before the onset of the cropping season, and cultivated mainly with maize during one or two years. They were not used as pasture before abandonment but occasional grazing cannot be ruled out.

Vegetation was sampled annually between August and October from 2003 to 2007. All woody and succulent plants ≥1 cm diameter at breast height (DBH, 1.3 m) were included. In each fallow four 20 × 5 m transects (subdivided in four 5 × 5 m quadrats) were marked; the transects were separated by 2 m corridors to minimize disturbance due to repetitive sampling. In each transect a size-stratified sampling was applied: all individuals ≥5 cm DBH were sampled in the four quadrats; individuals between 2.5 and 5 cm DBH were sampled in two quadrats, and individuals between 1 and 2.5 cm DBH were sampled in one quadrat only. All calculations were done by scaling the data to 1 ha. Stem DBH was measured to the nearest 1 mm and the exact measurement point was paint-marked for subsequent measurements. Two orthogonal crown diameters per individual were measured every other year to calculate crown areas. Recruits (new individuals reaching a 1 cm DBH) and dead individuals were recorded yearly. Further details of the sampling design can be found in Lebrija-Trejos et al. (2008).

Vegetation changes in forest diversity and structure were analyzed using Shannon's diversity index ( $H'$ ), Smith and Wilson's evenness index ( $E_{var}$ , Smith and Wilson, 1996), species richness (rarefied to 100 individuals using Ecosim, Acquired Intelligence Inc., Jericho, VT, USA), density of individuals, basal area (BA), and cover (expressed as the total sum of the individual crown areas). Data from the initial census (2003) were used to model chronosequence trends for each attribute; this was achieved by using the Levenberg–Marquardt iterative minimization algorithm (Moré, 1978) to fit a set of non-linear regression models having different maxima, minima and inflections points. Models included sigmoid, exponential and rational functions commonly used to describe developmental responses in time (e.g. Peña-Claros, 2003; Breugel et al., 2006; Yemefack et al., 2006). Akaike's information criterion corrected for small sample size was used to select the most parsimonious models. To analyze the differences between chronosequence models and individual-site pathways, the four-year individual-site trajectories were plotted together with the chronosequence-based models and their 95% confidence intervals, which show uncertainty in the trends modelled using the initial census data. Differences were then assessed by simple visual inspection and frequency calculations of (dis)agreement between modelled and repeated sampling trends. All calculations were done in GraphPad Prism v. 5.00 for Windows (GraphPad Software Inc., San Diego, CA, USA).

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