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Research article

Environmental filtering, local site factors and landscape context drive changes in functional trait composition during tropical forest succession

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A B S T R A C T

Second-growth forests provide an important avenue for at least partially recuperating biodiversity and ecosystem services in tropical regions. Yet, factors affecting changes in species and functional trait composition of trees during forest succession remain poorly understood. The environmental filtering hypothesis of community assembly predicts gradual successional changes in functional trait composition. However, differences in landscape conditions and local site factors can lead to idiosyncratic or divergent changes in species and functional composition.

We examine community assembly patterns of canopy trees and palms during natural regeneration using functional trait measurements and 18 years of annual vegetation dynamics data from six second-growth and two old-growth forest stands in northeast Costa Rica. We measured eight functional traits on 94 species, which cumulatively accounted for at least 80% of the abundance in each plot. Old-growth specialists had significantly lower leaf nitrogen and phosphorus content and significantly higher wood specific gravity than second-growth specialists. At the community level, specific leaf area, leaf nitrogen content, leaf dry matter content, and leaf toughness showed directional trends from more acquisitive trait values towards more conservative trait values. The landscape context was also an important driver of the successional trends within and among plots, as most functional trait patterns were influenced by the location of the plots within the matrix. Furthermore, the differential abundance of palms among stands strongly influenced functional trait differences among plots. After accounting for the effects of stand basal area and stand location, random plot effects explained an additional 45–90% of the variation in community-weighted mean functional traits. Local and landscape scale heterogeneity often influenced functional trait variation more strongly than stand basal area, suggesting that both stochasticity and environmental filtering influence species and functional turnover during succession.

1. Introduction

Regenerating forests globally comprise over half of the remaining tropical forests (FAO, 2010), providing a promising avenue for recuperating some of the biodiversity and ecosystem services that have largely been lost in human-modified landscapes (Chazdon et al., 2009). Tree species composition recovers relatively slowly during tropical succession and can vary considerably among similarly aged secondary forests depending upon soil conditions, land-use history and local seed dispersal (Brown and Lugo, 1990; Chazdon, 2003; Chazdon et al., 2007; Martin et al., 2013; Norden et al., 2015). These site-specific factors typically have long-term effects on the community structure and composition of regenerating forests (Mesquita et al., 2015; Norden et al., 2011).

Species composition is further influenced by the changing environmental conditions during forest development, including light availability (Denslow and Guzman, 2000; Guariguata and Ostertag, 2001; Nicotra et al., 1999) and soil fertility (Batterman et al., 2013; Guariguata and Ostertag, 2001; Lamb, 1980). Species' responses to these environmental changes are mediated by their functional traits, which reveal species-specific patterns of survival, potential resource acquisition, and actual resource allocation to leaves, wood, roots and seeds (Cornelissen et al., 2003; Díaz et al., 2004; Lasky et al., 2014; Menge and Chazdon, 2015; Westoby et al., 2002;

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Wright et al., 2004). Theoretically, under a purely functional model of community assembly, community composition is expected to be constrained to species with the appropriate traits to overcome the abiotic and biotic filters necessary to first arrive at a site, and then to establish and grow (Rees et al., 2001; Vile et al., 2006; Weiher and Keddy, 1999).

The stages of tropical succession are often described in terms of the composition of pioneers versus shade-tolerant species (Chazdon, 2008; Finegan, 1996), thus we expect plant functional traits to differ significantly among species with different successional affinities. Typically, early successional, short-lived pioneer species are classified as fast resource acquisition species, investing in cheap, short-lived leaves and low-density wood that provide a quick return on investment (Poorter and Bongers, 2006; Selaya and Anten, 2010; Westoby et al., 2002). Although the tissues of these acquisitive species are poorly protected from abiotic and biotic damage, their traits confer fast photosynthetic rates and high relative growth rates (Bazzaz and Pickett, 1980; Ellsworth and Reich, 1996). In contrast, shade-tolerant species often demonstrate resource conservation strategies. Species with resource conservation strategies have slow growth rates, but invest in long-lived tissues that are well defended against herbivores, pathogens and physical damage (Augspurger and Kelly, 1984; Coley, 1983; Reich et al., 2003). This generalized dichotomy between pioneers and shade-tolerant species has led ecologists to place species into ecological groups based on field observations rather than statistically rigorous classifications of habitat affinities (Poorter, 2007; Swaine and Whitmore, 1988). Here, we explicitly test whether leaf and stem functional traits differ significantly among species with different successional affinities, using a multinomial model approach to robustly classify species as second-growth specialists, old-growth specialists, or successional generalists based on their estimated relative abundances in second-growth and old-growth forests (Chazdon et al., 2011; Letcher et al., 2015).

Furthermore, we can determine the mechanisms that drive community assembly by assessing changes in community level functional trait values along successional gradients. When environmental filtering drives community assembly, the functional composition of forest communities is expected to shift directionally with stand age, in accordance with changing environmental conditions. Yet, local and landscape factors, such as topography and soils, proximity to forest patches, or stochastic factors such as dispersal limitation (Chazdon, 2008; Hubbell, 2001), can influence community assembly processes and cause significant site-specific variation in functional composition (Norden et al., 2015). The studies that have assessed stand-level functional trait dynamics of second-growth wet tropical forests (Craven et al., 2015; Dent et al., 2013; Lohbeck et al., 2013; Muscarella et al., 2015) have relied on a static chronosequence approach, in which temporal successional trends are inferred by measuring stands of different ages at a single time point. Although chronosequence studies provide useful insight into successional patterns (Prach and Walker, 2011), they often deviate from true vegetation dynamics because community reassembly patterns can be highly idiosyncratic, showing variation with land-use history and landscape factors that influence seed dispersal and establishment (Chazdon et al., 2007; Johnson and Miyanishi, 2008; Norden et al., 2015). Here, for the first time, we combine successional chronosequence and temporal data with functional trait measurements to test the relative influences of environmental filtering, site factors and landscape context on community assembly during natural regeneration.

We use 18 years of tree vegetation dynamics data in eight 1-ha forest monitoring plots to assess changes in functional trait composition during post-pasture succession in the lowland rainforest of northeastern Costa Rica. Our study provides a unique setting for testing the influence of site factors on functional composition, both because our long-term data allows us to examine trends within plots as well as across plots, and because our study plots are located within a heterogeneous landscape (Fagan et al., 2013). Although our second-growth stands shared similar land-use histories, they differ in landscape configuration and proximity to old-growth forests, which can influence species composition (Chazdon, 2008; Norden et al., 2015, 2009) and potentially functional composition. In our study area, proximity to old-growth forest favors abundant recruitment of canopy palms during succession (Sezen et al., 2009, 2007). Additionally, previous studies from our study location have shown that canopy palm abundance strongly drives patterns of compositional similarity among plots (Guariguata et al., 1997; Norden et al., 2009). Palms are often removed from community-level functional trait analyses because of the differences in leaf and stem construction between monocots and dicots (Dominy et al., 2008). However, palms are a dominant feature of tropical forest communities (Marín-Spiotta et al., 2007; ter Steege et al., 2013), and they play an important functional role in the forest. The unique columnar architecture of arborescent palms inhibits liana growth and limits the amount of light reaching the forest floor (Salm et al., 2005), and their fruits are an important food source for large mammals such as peccaries and primates, and large birds, such as toucans (Queenborough et al., 2012). Palm abundance can directly influence functional composition if the differences in the construction of palms and dicots result in differences in functional traits. Furthermore, as the foraging activities around the base of palms can alter plant community composition (Queenborough et al., 2012), the abundance of palms in the landscape may have an indirect influence on functional composition.

Our study focuses on the intermediate stages of succession, spanning the stem exclusion and understory reinitiation phases of tropical forest succession (Chazdon, 2008). Whereas pioneer trees with acquisitive functional traits dominate the initial, stand initiation phase of succession (lasting up to ~10–15 years after disturbance subsides), we focus on the two subsequent phases of succession, which contain an increasing diversity of species and functional types and provide deeper insight into the transition from second-growth forest to old-growth forest. Although the exact timeline of these stages varies regionally and is influenced by land-use history and other factors, in the Caribbean lowlands of Costa Rica the stem exclusion phase spans approximately 10–25 years after disturbance, and the understory reinitiation phase begins approximately 25 years after disturbance and can last for up to 200 years (Chazdon, 2008). Our study also includes old-growth forests, which serve as reference points for the final stages of succession. To understand the driving mechanisms of community assembly along this wet tropical forest successional gradient, we address the following questions:

1 Do tree species with statistically established successional habitat affinities exhibit the expected trends in ecophysiological functional traits? Specifically, do second-growth specialists have fast resource acquisition traits, old-growth specialists have resource conservation traits, and generalist species have intermediate traits? Do generalist species show more intraspecific trait variation than second-growth and old-growth specialists?
2 Does functional composition change directionally along the successional gradient, supporting a deterministic view of community assembly? What is the relative importance of stand age, local site factors, and landscape context in driving functional community assembly during succession?
3 How does the abundance of canopy palms influence the successional patterns of functional community assembly within and across plots?