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Structure and community composition in a tropical forest suggest a change of ecological processes during stand development

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ABSTRACT

Ecological theories assume that ecological processes change during stand development. This change should be reflected in patterns of tree and crown allometries, stand demography and community composition. Empirical tests of these predictions have largely concentrated on temperate forests. Here, we ask whether these expectations also hold in tropical forests. We established eight permanent inventory plots of different ages in a tropical forest in Thailand, and measured dbh, crown architecture and community composition. We then tested whether differences in (1) allometries, (2) size structure, (3) stand structure and (4) community composition between plots are consistent with expectations from succession theory. In particular, we tested if tree and stand patterns conform to the expectation that competition intensity is highest during intermediate development stages, and that species specialize into particular successional niches. We find that the empirical patterns in the plots are compatible with both assumptions. Observed dbh-height and crown allometries, as well as stand attributes, suggest that trees respond to denser packing in the intermediate development stage (stem exclusion stage) by increased investments in height growth, presumably because of strong resource competition, particularly for light. Packing and competition seems less pronounced in earlier and later stages. An analysis of community composition shows that species composition clustered with development stages, suggesting a specialization into successional niches. In conclusion, stand attributes of the tropical plots used in this study largely conform to the predictions of forest stand development theories that have so far mainly been tested in temperate forests. We did not find evidence for qualitative differences between tropical and temperate stand development.

1. Introduction

Tropical forests worldwide have been subject to major disturbances by logging, land clearing for cultivation and pasture, as well as slash-and-burn agriculture for at least four decades (Chazdon, 2014). In many parts of the world, these disturbances continue at alarming rates, but in some areas, protection and restoration activities have initiated forest regeneration. To support these regeneration processes, as well as to better understand the ecology of tropical forests in general, we need to better understand the ecological processes that govern stand development.

Research on stand development in tropical forests has a long history (Budowski, 1965; Whitmore, 1975; Finegan, 1996). Most conceptual theories for describing this phenomenon, however, were developed and tested for temperate forests (Oliver and Larson, 1996; Franklin et al., 2002; Halpern and Lutz, 2013; Bartels et al., 2016). A common property of most of these theories is the idea that a forest stand undergoes different development stages during succession, and that ecological processes change in the course of this process. Oliver and Larson (1996) proposed a model of temperate forest stand dynamics with four stages: (1) stand initiation, (2) stem exclusion, (3) understory reinitiation, and (4) old growth. The classification criteria for these stages concentrate on processes and structural changes during stand development, rather than species diversity and composition. To test this model, one would thus need to test if there is indeed evidence for structural changes caused by resource competition during stand development that are in agreement with the predictions this and similar models (Oliver and Larson, 1996; Franklin et al., 2002; Halpern and Lutz, 2013; Bartels et al., 2016).

As an example of such a prediction, the model by Oliver and Larson

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(1996) implies that the stand initiation stage should be associated with lower resource competition (particularly for light and space), and with the potential presence of facilitating processes, because of the presence of open spaces and remnant trees that can provide shade, moisture and seed sources (Peterson and Carson, 2008; Chazdon, 2014). Competition should then increase during the stem exclusion stage, because of higher density and lower recruitment of understory tree species caused by increasing resource limitation, resulting in self thinning among canopy trees (Oliver and Larson, 1996; Franklin et al., 2002; Bartels et al., 2016). Also, the dense canopy-packing (with canopy space limitation) should reduce light penetration into the deeper forest layers, which should affect demographic processes such as recruitment (Nicotra et al., 1999; Montgomery and Chazdon, 2001; Uriarte et al., 2016) as well as tree and crown architecture. One would therefore expect that crown projection area should be lower, and that trees compete for light by investing mainly in height growth, resulting in steeper diameter-height allometries. For the late-successional or old-growth stage, in which gap formation occurs randomly, a mix of ecological processes should occur, and no dominant structural or architectural pattern is expected.

When considering tropical forests, the question arises whether the patterns described by Oliver and Larson (1996) would also be applicable to these much more diverse ecosystems. One would expect differences, for example, if the relative importance of different ecological processes differs between the two zones, or if some evolved functional strategies (climbers, emerging trees) can only exist in one of the zones (Ostertag et al., 2014). Whether the temperate the stand development model is transferable to tropical forests was discussed already by Oliver (1992), as well as more recently by (Chazdon, 2014; Uriarte et al., 2016). However, to the best of our knowledge, so far no studies have quantitatively examined if tropical forest structure conforms with temperate stand development theory throughout all stages of stand development in tropical forests.

The objective of this study was to test if the general expectations of temperate-forest succession models also hold for a species-rich tropical forest, and in general to better understand the processes of stand development after a major disturbance. To that end, we established eight forest plots in Khao Yai National Park, Thailand, in stands of different ages regenerated from abandoned fields imbedded in a matrix of old growth or relatively mature forest. So far, most studies of tropical succession have been conducted in human-dominated areas (Arroyo-Rodriguez et al., 2017), which usually creates problems with dispersal limitation because of extirpation of seed dispersers (Corlett, 2007) or matrix complexity (Arroyo-Rodriguez et al., 2017). Our study site offers rare conditions because virtually all original seed dispersers still exist in viable populations (Lynam et al., 2006.).

Our analysis addresses the following questions: (1) How do tree and crown architecture as well as demography change during stand development after a single large-scale disturbance? (2) Are those differences in agreement with the expectation that resource competition peaks at intermediate stand development stages? (3) Is there evidence for species specialization to particular stand development stages?

2. Material and methods

2.1. Study area

The study area is located in the inner part of Khao Yai National Park in central Thailand (Fig. 1). The area consists of a mosaic of secondary forest (regenerated from old fields *ca.* 15–40 years old) and old growth forest, covering approximately 50 km^2 (14°23′–14°27′N; 101°20′–101°24′E). The forest is seasonal evergreen, ranging from 720 to 890 m in altitude. Annual precipitation averages about 2100 mm, and annual minimum and maximum temperatures average 19 °C and 28 °C, respectively. The dry season lasts from November to April or May. Prior to the establishment of the park, parts of the area were used for low-intensity agricultural activity, consisting mostly of upland rice and subsistence crops. When the national park was established in 1962, all local settlers were relocated outside the park. Since then, some of the more accessible abandoned fields have been maintained by fires in the dry season, set intentionally by park managers. Remote fields, on the other hand, started to regenerate as soon as they escaped burning for one or two years. The result is a landscape mosaic consisting of fields and forest patches of different ages, surrounded by old growth or relatively mature forest.

2.2. Site selection and forest inventory design

Site selection was guided by the aim of finding several regenerating stands that would allow the establishment of inventory plots in (1) early (stand initiation) stage, (2) intermediate (stem exclusion) stage, and (3) old growth stage. We aimed at having triples of different stages in close vicinity to minimize the effect of other environmental factors and variation in species composition in the analysis. However, we only found suitable plots in the stem exclusion and the old growth stages in close proximity (Fig. 1). The plots selected in the stand initiation stage were somewhat apart from the other plots. Forest age was estimated by interviewing old rangers and using Landsat remote sensing data as 15–20 for the early and 35–40 years for the intermediate plots. Judging from tree sizes, the surrounding old-growth forest was at least 200 years old. After identification of suitable areas, eight 60 m × 80 m (0.48 ha) plots were established (Fig. 1). For the tree inventory, each plot was subdivided into 12 quadrats of size 20 m × 20 m in a 4 × 3 pattern. We measured, tagged, mapped and identified all trees with diameter at breast height (dbh) > 4 cm, between March and May 2013.

2.3. Measurement of tree architecture

To measure tree architecture (see ecological hypotheses in the next section), we used stratified random subsampling to obtain 40–50 individuals, with the constraint that all height classes were evenly represented. The goal of the stratification was to provide a balanced size distribution for statistical analysis. For all selected individuals, we measured height at crown top and the lowest living branch of the crown. Tree individuals with heights < 5.4 m were measured with a pole, whereas individual trees with height ≥5.4 m were initially measured with a laser range finder (Nikon Forestry 550) in 2013. The experience from this first measurement campaign suggested that the rangefinder measurements can be inaccurate for tall trees located in a dense canopy, because the laser beam can easily be interrupted by other leafs before reaching the real crown top. We therefore remeasured all tall trees (> 7 m) with a Vertex III (Haglöf, Sweden) in May 2014. In the data analysis, we used the Vertex measurement when it was available. We defined crown length as the difference between crown top and lowest branch. Crown shape was visually classified into four types: cone-like, spherical, oval (ellipse) and flat (Supplementary material S1). The shape was used for the calculation of the crown volume. Crown projection area was recorded using four crown diameter measurements at 90° angles to each other. Displacement of the crown center was measured relative to the trunk base (see more detail in Supplementary material S1).

2.4. Ecological hypotheses and statistical analysis

Based on assumptions from the stand development model of Oliver and Larson (1996), we summarize hypotheses and expectations for four main aspects of succession below: (1) allometry, (2) size structure, (3) stand structure, and (4) community composition. For each of these aspects, we specified one or several statistical tests with which to confront our field data. All statistical scripts are provided in Supplementary material S4.