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Original article

Field observed relationships between biodiversity and ecosystem functioning during secondary succession in a tropical lowland rainforest

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A R T I C L E I N F O

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ABSTRACT

The relationship between biodiversity and ecosystem functioning (BEF) is one of the most concerned topics in ecology. However, most of the studies have been conducted in controlled experiments in grasslands, few observational field studies have been carried out in forests. In this paper, we report variations of species diversity, functional diversity and aboveground biomass (AGB) for woody plants (trees and shrubs) along a chronosequence of four successional stages (18-year-old fallow, 30-year-old fallow, 60-year-old fallow, and old-growth forest) in a tropical lowland rainforest recovered after shifting cultivation on Hainan Island, China. Fifty randomly selected sample plots of 20 m \times 20 m were investigated in each of the four successional stages. Four functional traits (specific leaf area, wood density, maximum species height and leaf dry matter content) were measured for each woody plants species and the relationships between species/functional diversity and AGB during secondary succession were explored. The results showed that both plant diversity and AGB recovered gradually with the secondary succession. Consistent with many controlled experimental results in grasslands, our observational field study confirms that ecosystem functioning is closely related to biodiversity during secondary succession in species rich tropical forests.

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1. Introduction

Effects of biodiversity on ecosystem functioning have emerged as one of central issues in ecological and environmental sciences (Loreau, 2010). A series of reviews and meta-analyses about effects of biodiversity on ecosystem functioning based on a broad array of studies from marine, terrestrial and freshwater ecosystems (Hooper et al., 2005; Balvanera et al., 2006; Stachowicz et al., 2007; Cardinale, 2012) show that ecosystem functions are significantly influenced by different aspects of biodiversity. However, most of them have been conducted in grassland by manipulating combinations of herbaceous species richness. Due to the limited numbers of species and the controlled environment, the consistency of these experimental results with the actual field situations still need to be proven. Actual field ecosystems are far more complex than the ones designed by controlled experiments. Up to now, few studies about effects of biodiversity on ecosystem functioning have been done in the actual natural ecosystems, especially in complex ecosystems such as the tropical rainforests. The complexity in natural ecosystems may alter our perception of biodiversity effects on ecosystem functioning obtained from experimental studies (Hillebrand and Matthiessen, 2009).

In analyzing the relationships between biodiversity and ecosystem functioning, diversity based only on taxonomic diversity may provide an incomplete view of biodiversity and it does not take into account the differences of ecological strategy and function among species (Petchey et al., 2004; Reiss et al., 2009). A step further in biodiversity assessment needs to consider the role of each species in ecosystems or species responses to environmental conditions, which is actually what the functional view of biotic communities aims to quantify (McGill et al., 2006). Functional traits are defined as the morphological, physiological, or phenological traits which impact fitness via their effects on growth, reproduction and survival, the three components of individual performance (Violle et al., 2007). Some studies demonstrated that effects of biodiversity on ecosystem functioning mainly attributed to







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functional traits of species and species interactions (such as direct or indirect competition, facilitation) rather than species richness per se (Díaz et al., 2007; Quétier et al., 2007). Traits-based approaches can effectively link plant physiological, morphological and life history characteristic with environmental change and predict the impacts of species composition on ecosystem functioning in different spatial and temporal scales (Webb et al., 2010). Functional diversity, the value and range of functional traits of the organisms present in a given ecosystem, has important effects on ecosystem processes (Falster et al., 2011). Studies related with 'functional diversity' have been increasing rapidly, especially in the last decade (Cadotte, 2011).

A series of influential field experiments, conducted primarily in grasslands, demonstrated that the identity and number of plant species in a system could affect primary productivity and biomass accumulation (Cardinale, 2012). Furthermore, functional diversity could provide better description of the effects on ecosystem functioning than species diversity since species-ecosystem process relationships are assumed to be mediated via functional traits (Suding et al., 2008; Ruiz-Jaen and Potvin, 2011). However, few observational studies have been carried out in actual natural sites to test whether ecosystem function is related with the biodiversity (including species diversity and functional diversity) or not. Tropical forest is characterized by its rich array of species and high level of primary productivity. Observations on the relationship between biodiversity and ecosystem functioning in tropical forests might help to test the validity of those conclusions got from grassland experiments when applied to species diverse forest ecosystems. In this paper, we utilized field observational data to test the effects of biodiversity on aboveground biomass along a successional chronosequence in a tropical lowland rainforest. We address specifically three questions as follows: (1) whether species/functional diversity and stand aboveground biomass increased with the recovery of the tropical lowland rainforest? (2) whether biodiversity and aboveground biomass had any correlations in each stage of secondary succession? And (3) what were the possible mechanisms driving the relationships between diversity and aboveground biomass during the secondary forest succession?

2. Materials and methods

2.1. Study sites

The study area was in the Bawangling forest region (BFR, $18^{\circ}52'-19^{\circ}12'$ N, $108^{\circ}53'-109^{\circ}20'$ E) on Hainan Island, south China. It is at the northern edge of Asian tropical forest (Ding et al., 2012). The BFR is ca500 km², with an elevation range of ca 100–1654 m. The mean annual temperature is 23.6 °C, and annual precipitation is 1677 mm, with a distinct wet season from May to October and a dry season from November to April.

Before 1994, tropical forests on Hainan Island have experienced extensive deforestation by logging and shifting cultivation. The deforestation rate in this area is higher than the average deforestation rate of the world, due to the shortage of timbers and agricultural lands (Zang et al., 2004). Most of the primary tropical lowland forests in low-elevation areas of Hainan Island have been converted to shifting cultivation lands. After a relative short period of cultivation, the lands were usually abandoned due to soil erosion of the lands, and natural recovery of vegetation began. Consequently, secondary forests of different recovery degrees or successional stages can be found in the low-elevation areas of Hainan Island, which affords a good site to study secondary forest succession by using a space for time substitution approach although using a chronosequence may not be the same as using a succession in real time.

The field investigation was conducted in the tropical lowland rainforest which had naturally recovered after shifting cultivation in four stages of succession (18-year-old fallow, 30-year-old fallow, 60-year-old fallow, old-growth forest). In each stage of succession, we sampled 50 plots ($20 \text{ m} \times 20 \text{ m}$) randomly. Information on the history of land use of the plots was obtained from management records of Bawangling Bureau of Forestry of Hainan. These plots have similar topographic conditions. They are located in low hills with slopes of about 15°, and their elevations range from 412 to 626m.

2.2. Species and traits

Field sampling was conducted in these plots of tropical lowland rainforests from May to July in 2010. All trees and shrubs with diameter at breast height (dbh) > 1 cm in each plot were identified and measured. Species names were recorded in accordance with Flora Reipublicae Popularis Sinicae (Editorial Committee of Flora of China, 2004). All species were sampled to measure functional traits data. For rare species (<10 individuals per ha), all individuals were sampled and over ten individuals per common species (>10 individuals per ha) were sampled. Totally, 6663 individuals of 274 species were measured. For each individual, two to five recentlyexpanded leaves, including petioles and rachises of compound leaves were collected (Cornelissen et al., 2003). Leaf surface area was measured with a leaf area meter (LI-COR 3100C Area Meter, LI-COR, USA). Laminar dry mass was measured by drying to constant mass at 60 °C (around 72 h), and specific leaf area (SLA, $cm^2 g^{-1}$) was calculated for each lamina as the ratio of leaf surface area to leaf mass. Leaf dry matter content (LDMC, $g g^{-1}$) was the oven-dry mass divided by its fresh mass. To characterize species wood density (WD, g cm⁻³), which is more laborious, we sampled branches $(1 \text{ cm} \le \text{dbh} \le 2 \text{ cm})$ from corresponding individuals which had been sampled for leaf traits. We removed the pith, phloem, and bark, measured fresh volume by water displacement and determined dry mass after drying for 72 h at 70 °C (Cornwell et al., 2006). Meanwhile, we chose ten species of hardwood and corkwood respectively, ten individuals per these species were sampled nearby the study sites, and cores of stem were taken with an increment borer (Haglof Increment Borer, Sweden) after sampling of branches. We found that the core density linearly related to the branch density for hardwood ($\rho_{core} = 1.054 \rho_{branch}$, $r^2 = 0.946$, p < 0.0001) and for corkwood ($\rho_{core} = 1.235 \rho_{branch}$, $r^2 = 0.925$, p < 0.0001). Data of maximum height (Hmax, m) came from the Flora of China (www. efloras.org) and our field observations. These four functional traits were selected because they are among the most important and commonly studied traits and are important for aboveground biomass.

2.3. Species and functional diversity

We examined species diversity and functional diversity in each plot. In this paper, we characterize species diversity by species richness (S), Shannon Weaver index (H) and Pielou's evenness (J). For functional diversity, we considered three principal facets of functional diversity (Mouchet et al., 2010) and calculated them for all four traits together. Functional richness (FRic) is estimated by the convex hull volume, an n-dimensional measure of the volume of trait space occupied by species in a community (Cornwell et al., 2006). Functional evenness (FEve) represents the regularity of distribution in abundance in this volume. Functional divergence (FDiv) represents the divergence in the distribution of the species traits within the trait volume occupied. We estimated them using the FD package in R with the function dbFD (Laliberté and Legendre, 2010). Download English Version:

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