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Scale-dependence of aboveground carbon accumulation in secondary forests of Panama: A test of the intermediate peak hypothesis

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ABSTRACT

Accumulation of aboveground carbon is one of the most important services provided by tropical secondary forests—a land-cover type that is increasing in importance globally. Carbon accumulates rapidly for the first 20 years of succession, but few studies have considered forests older than 20 years, and the available data do not yield a consistent pattern. Two alternative hypotheses have been proposed: (1) an asymptotic increase, with the highest carbon stocks occurring in the oldest stands, and (2) an intermediate peak, caused by roughly synchronous tree maturity (and thus high carbon stocks) after which time treefall gaps cause carbon stocks to regress. Here we revisited a well-studied tropical moist forest chronosequence in Barro Colorado Nature Monument, Central Panama, consisting of 35, 55, 85, and 115-year-old stands, as well as old-growth stands, to determine whether past evidence for the intermediate peak hypothesis was influenced by the spatial limitations of the field plots used to assess forest structure. We used airborne LiDAR (light detection and ranging) to measure carbon stocks at the scale of the original transects (0.16 ha), in surrounding forest of the same age (up to 20 ha), and at a landscape scale incorporating thousands of hectares not previously measured. We also compared forest structure as measured in three dimensions by LiDAR, considering vertical and horizontal variation in canopy organization, as well as the abundance of treefall gaps. Our results suggested a strong scale-dependence of aboveground carbon accumulation, supporting the intermediate peak hypothesis at the fine scale of the 0.16-ha transects, but an asymptotic model at the landscape scale incorporating thousands of hectares. Further analyses of forest structure suggest that both the limitations of small plots and intrinsic scaling of forest structure and carbon dynamics account for the scale-dependence of aboveground carbon accumulation in this secondary forest matrix.

1. Introduction

After human abandonment of forest clearings in the tropics, a dynamic recovery of forest structure begins. Left uninterrupted, succession will ultimately lead toward maturity (Ewel, 1980), but in the interim, the composition, structure, and function of secondary forests differ markedly compared to primary forests. A valuable service provided by secondary forests is their recovery of carbon storage. Although tropical forests store 350 Pg of carbon in their aboveground biomass—more than any other biome (Fischlin et al., 2007)—the contribution of secondary forests to the carbon budget of the tropical forest biome remains highly uncertain, particularly the role of older secondary forests that have been little studied. One major review by Brown and Lugo (1990) established that aboveground carbon density (ACD, units of Mg C ha^{-1}) increases rapidly for the first 20 years of succession, but found that limited data were available for forests in later stages of ACD accumulation, and that variability was high. Although more than 20 years have elapsed since the publication of this seminal review, our understanding of late-stage carbon accumulation in tropical secondary forests remains limited (Fig. 1)—as few studies have considered forests older than 20 years (Alves et al., 1997; Kotto-Same et al., 1997; Hughes et al., 1999; Hashimotio et al., 2000; Johnson et al., 2001; Kenzo et al., 2010; Yepes et al., 2010).

Peet (1999) reviewed three models for biomass (ACD) accumulation in secondary forests: (1) an asymptotic increase to maximal ACD in the oldest stands, (2) an intermediate peak, caused when

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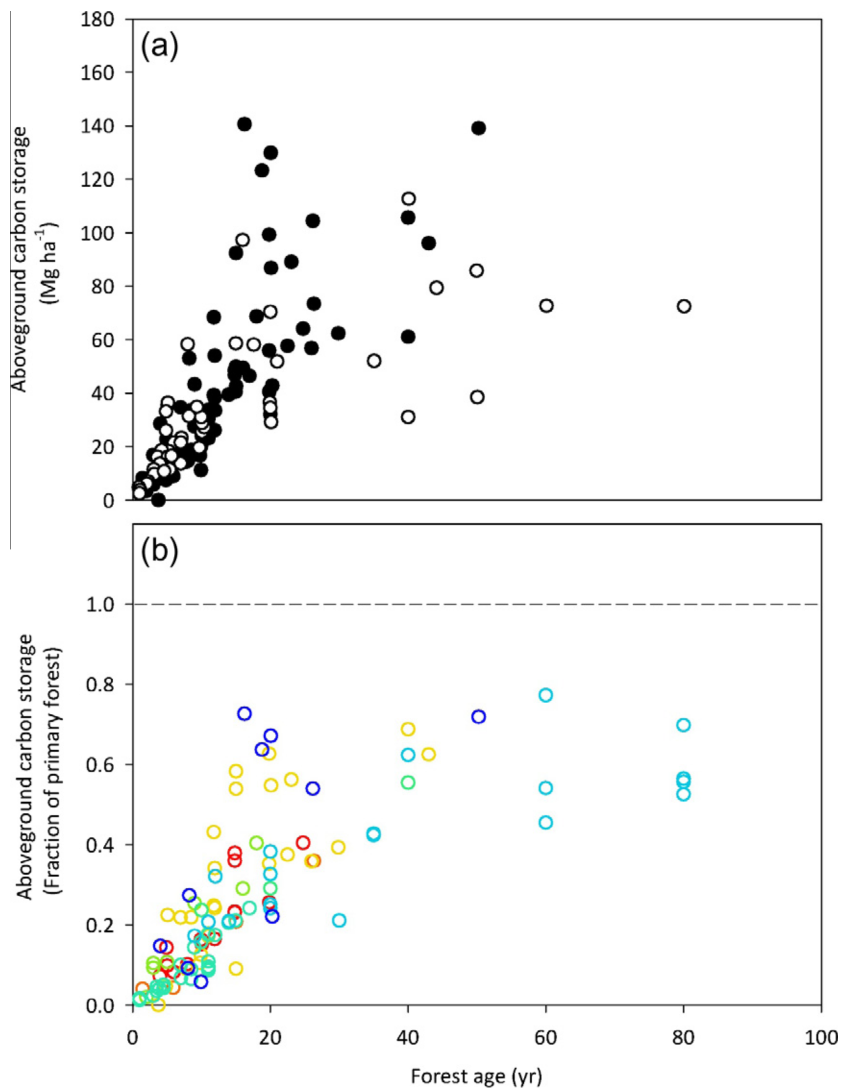

Fig. 1. (a) Results of previous chronosequence studies in tropical secondary forest carbon accumulation including a review by Brown and Lugo (1990) (open circles) and eight subsequent studies as cited in the text (closed circles). (b) Plot-scale carbon accumulation on a fractional basis relative to a local primary forest carbon stock estimate for a subset of studies; these include eight recent studies cited in text, plus Saldarriaga et al. (1988), which accounted for the oldest sites utilized by the Brown and Lugo review. In this case, the sites are colored by mean annual rainfall, ranging prismatically from 1600 (red) to 4000 mm (blue). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

most patches are occupied by large trees—after which time some of these trees begin to die at different rates and ACD regresses to a lower level, and (3) a series of oscillations around an intermediate value caused by stand-synchronous dieback. All three models have been demonstrated using chronosequence studies in the tropics (for ACD, biomass, or basal area), with most studies demonstrating either an asymptotic increase or an intermediate peak (citations in Peet, 1999). In rare cases, some tropical forests show oscillations caused by synchronous dieback (e.g., endemic *Metrosideros polymorpha* forests in the Hawaiian Islands; Mueller-Dombois and Fosberg, 1998)—though such oscillations are more common in boreal forests (Larsen, 1980). Therefore, most mainland tropical forest studies have supported either the asymptotic increase hypothesis or the intermediate peak hypothesis.

Although demonstrated empirically, the evidence for the intermediate peak hypothesis may be confounded by the small spatial scale common in chronosequence studies. Most mature tropical forests are several centuries old, prohibiting ecological observation of the changes that may take place over the course of succession from disturbance to maturity. This challenge has frequently been confronted with a space-for-time substitution (chronosequence). In an attempt to assess forest properties along the entire chronosequence, plot size is often necessarily sacrificed to add additional age categories, which creates the possibility that a plot within a given age category may be smaller than typically needed to capture local forest structural variation (generally, 0.25 ha; Clark and Clark, 2000).

We used airborne Light Detection and Ranging (LiDAR) to assess changes in forest structure and ACD within a previously studied chronosequence in the Barro Colorado Nature Monument (BCNM; Denslow and Guzman, 2000; DeWalt et al., 2000). LiDAR relies on emitted laser pulses to measure the distance between objects, allowing three-dimensional detection of forest structure. Airborne LiDAR instruments can be operated over many thousand hectares of forest per day. Thus, we were able not only to examine changes in forest structure and carbon stocks in previously-studied plots, but also to extend the spatial scale of each time-step of the chronosequence (i.e., patches of the same forest age), and develop an improved understanding of the three-dimensional nature of forest structure. In revisiting the BCNM chronosequence, we expand on previous analyses that were limited in spatial extent by design. Our goals were to (1) determine whether the intermediate peak