

GfÖGfÖ Ecological Society of Germany, Austria and Switzerland

Basic and Applied Ecology

www.elsevier.com/locate/baae

Basic and Applied Ecology 16 (2015) 239–249

Relationships between tree species richness, evenness and aboveground carbon storage in montane forests and miombo woodlands of Tanzania



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Received 3 February 2014; accepted 30 November 2014 Available online 5 December 2014

Abstract

Understanding how carbon storage and tree diversity are related in forests and woodlands is crucial for a sustainable flow of ecosystem goods and services. The goal of this study was to determine how tree species richness, evenness and environmental factors influence aboveground live tree carbon stocks (AGC) in two tropical vegetation types in Tanzania. We surveyed trees and sampled soil from 222 vegetation plots ($20 \text{ m} \times 40 \text{ m}$) in montane forests (n = 60) and miombo woodlands (n = 162). We used a multimodel inference approach to determine how AGC related to tree species richness, evenness and environmental factors, and linear mixed effect models to test the role of tree sizes on the AGC-richness and evenness associations. AGC were related unimodally to tree species richness and evenness in the montane forest. Likewise, AGC in the miombo woodlands was positively related to tree species richness. AGC from small trees were related unimodally to tree species richness in both vegetation types. Apparently the AGC had both monotonically increasing and decreasing associations with all abiotic environmental factors in both vegetation types. We emphasize that both tree size, number of multi-stemed trees and environmental factors have an important role in determining how AGC are related to richness and evenness. Finally, management of montane forests and miombo woodlands of Tanzania to enhance ecosystem benefit, such as AGC, will require strategies that consider tree sizes, tree species richness, evenness and underlying environmental and disturbance factors.

Zusammenfassung

Zu verstehen, in welcher Beziehung Kohlenstoffspeicherung und Baumdiversität in Wäldern und Gehölzen zueinander stehen, ist entscheidend für einen nachhaltigen Fluss von Ökosystemprodukten und -dienstleistungen. Das Ziel dieser Untersuchung war zu bestimmen, wie Baumdiversität und -evenness sowie Umweltfaktoren die oberirdischen Kohlenstoffvorräte in lebenden Bäumen (AGC) in zwei tropischen Vegetationstypen in Tansania beeinflussen. Wir untersuchten Bäume und nahmen Bodenproben auf 222 Probeflächen ($20 \text{ m} \times 40 \text{ m}$) in Bergwäldern (n = 60) und in Miombo-Baumsavannen (n = 162). Wir wählten einen Mehr-Modell-Analyse-Ansatz um zu bestimmen, wie der AGC mit der Baumdiversität und -evenness sowie Umweltfaktoren verknüpft ist, und lineare gemischte-Effekte-Modelle, um den Einfluss der Baumgröße auf die Beziehung zwischen

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AGC und Artenreichtum bzw. AGC und Evenness zu testen. Der AGC war im Bergwald unimodal mit Baumartenreichtum und -evenness verknüpft. Ebenso war der AGC in der Miombo-Baumsavanne positiv mit dem Baumartenreichtum verbunden. Der AGC von kleinen Bäumen war in beiden Vegetationstypen unimodal mit dem Artenreichtum der Bäume verknüpft. Offenbar hatte der AGC in beiden Vegetationstypen sowohl monoton ansteigende als auch abfallende Beziehungen mit allen abiotischen Umweltfaktoren. Wir betonen, dass sowohl Baumgröße, Anzahl der mehrstämmigen Bäume und Umweltfaktoren eine wichtige Rolle für die Beziehung zwischen AGC und Artenreichtum bzw. Evenness spielen. Um den Ökosystemnutzen, z.B. AGC, zu steigern, wird das Management der Bergwälder und Miombo-Baumsavannen in Tansania Strategien erfordern, die Baumgröße, Artenreichtum, Evenness und zugrundeliegende Umwelt- und Störungsfaktoren berücksichtigen.

Keywords: Biodiversity; Species dominance; Ecosystem services; Biomass production; Soil-nutrients

Introduction

Trees play major roles in carbon storage and forest ecosystem functioning (Lopez-Toledo et al. 2012). Forest plant diversity has the potential to modify the rate of carbon fluxes and to mitigate effects of climate change (Diaz, Hector, & Wardle, 2009). At a landscape scale, tree species diversity interacts with water, soil nutrients, litter quality and quantity, and light availability to govern carbon input into the ecosystem (Chapin, Matson, & Mooney 2002). However, current rates of forest degradation, deforestation and a general decline in tree species diversity have influenced forest ecosystem processes, such as carbon cycling (Butchart et al. 2010). Species richness may be strongly associated with carbon storage (Strassburg et al. 2010) and richness and biomass may relate positively, negatively or unimodally (Ruiz-Jaen & Potvin, 2011; Grace, Adler, Harpole, Borer, & Seabloom 2014). However, few studies have determined how carbon storage changes with plant species evenness (Collet, Ningre, Barbeito, Arnaud, & Piboule 2014; Orwin, Ostle, Wilby, & Bardgett 2014). Primarily two hypothetical mechanisms (complementarity effect and selection effect hypotheses) underline how plant species diversity and biomass production are related (Tilman et al. 1997; Cardinale, Hillebrand, Harpole, Gross, & Ptacnik 2009). In diverse plant communities, individuals optimize resource use through niche partitioning, unlike communities dominated by few plant species, where resource allocation will largely depend on the dominant species (Cardinale et al. 2009; D1az et al., 2009). According to Gross and Cardinale (2007), resource supply can affect species richness and in turn can affect biomass production. However, the causality in the richness-biomass production association, especially in natural vegetation at local and regional scales, is still unclear (Oksanen 1996; Grace et al. 2014).

Contrasting results on the association between plant biomass and plant species richness indicate the complexity underlying mechanisms and a need for further studies (Willig 2011). Although Strassburg et al. (2010) found that carbon stocks are related to plant diversity on a global scale, attempts to generalize this pattern has been challenging and

consequently raised a debate among ecologists (Grace et al. 2014). Lack of consistent pattern on how biomass production and richness are related could be due to spatial and temporal interacting factors, such as physiographic, edaphic, climatic and disturbance conditions (Chisholm et al. 2013). The use of multiple measures, such as richness, evenness, diversity and environmental factors, may enhance our understanding of how carbon storage and plant species richness are related in various ecosystems (Willig 2011). Moreover, although tree size has a large influence on aboveground carbon storage (Sist, Mazzei, Blanc, & Rutishauser 2014), to our knowledge no study has focused on how tree size can influence the way aboveground carbon stocks are related to richness and evenness.

This study examines how tree Shannon diversity, richness and evenness are related to aboveground live tree carbon stocks (AGC) under different abiotic environmental conditions in montane forests and miombo woodlands in Tanzania. Based on the biodiversity-ecosystem function theory (Cardinale et al. 2009), we used AGC as a response variable with measures of tree species richness, evenness and abiotic environmental factors (edaphic and disturbance) as explanatory variables. We ask the following questions: (1) Do AGC relate to tree species richness and evenness in the two vegetation types? (2) Do environmental factors affect how richness and evenness are related to AGC in the two vegetation types? (3) Does tree size determine how AGC are related to richness and evenness in the two vegetation types?

Materials and methods

Study area

We studied a montane forest on the northern rift zone in the Hanang district and miombo woodlands in the Kilombero, Kilolo, Mufindi, Iringa, Mbeya, Rufiji, Kilwa and Chunya districts in Tanzania (Fig. 1). The Hanang forest occurs at an altitude rage of 1980 to 3300 m with a wide range of forest types, from montane to upper montane and dry montane forests (Lovett & Pocs 1993). The dominant

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