Science of the Total Environment 598 (2017) 38–48

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Disentangling the effects of species diversity, and intraspecific and interspecific tree size variation on aboveground biomass in dry zone homegarden agroforestry systems

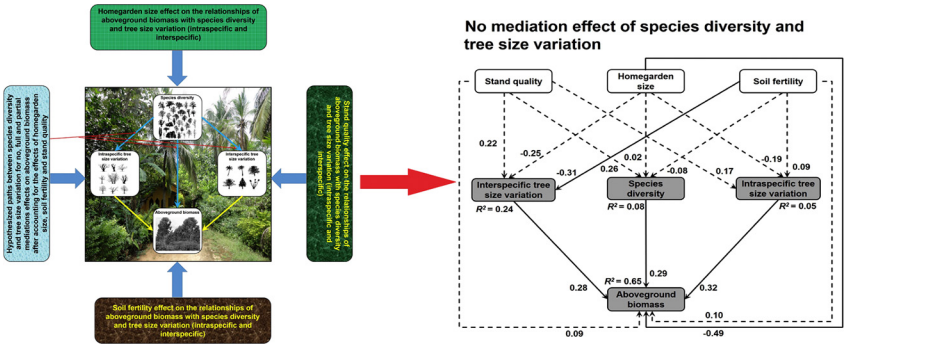
Arshad Ali [a,b,c], Eskil Mattsson [d,*]

[a] School of Ecological and Environmental Sciences, East China Normal University, Shanghai 200241, China
[b] Forest Ecosystem Research and Observation Station in Putuo Island, Zhoushan, Zhejiang 316100, China
[c] Tiantong National Forest Ecosystem Observation and Research Station, Ningbo 315114, Zhejiang, China
[d] Centre for Environment and Sustainability, Chalmers University of Technology, 412 96 Göteborg, Sweden

HIGHLIGHTS

- Species diversity, and intraspecific and interspecific tree size variation did not affect each other.
- Aboveground biomass was directly affected by species diversity and tree size variation (the no mediation effect).
- Intraspecific tree size variation needs to be considered in the relationship of biodiversity and ecosystem functions.
- Statistical modelling reveals mechanisms for testing complex paths of biodiversity – aboveground biomass relationships.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 12 January 2017
Received in revised form 18 April 2017
Accepted 18 April 2017
Available online xxxx

Editor: Elena PAOLETTI

Keywords:
Aboveground biomass
Agroforestry
Biodiversity
Species diversity
Structural equation models
Tree size variation

ABSTRACT

The biodiversity – aboveground biomass relationship has been intensively studied in recent decades. However, no consensus has been arrived to consider the interplay of species diversity, and intraspecific and interspecific tree size variation in driving aboveground biomass, after accounting for the effects of plot size heterogeneity, soil fertility and stand quality in natural forest including agroforests. We tested the full, partial and no mediations effects of species diversity, and intraspecific and interspecific tree size variation on aboveground biomass by employing structural equation models (SEMs) using data from 45 homegarden agroforestry systems in Sri Lanka. The full mediation effect of either species diversity or intraspecific and interspecific tree size variation was rejected, while the partial and no mediation effects were accepted. In the no mediation SEM, homegarden size had the strongest negative direct effect ($\beta = -0.49$) on aboveground biomass ($R^2 = 0.65$), followed by strong positive direct effect of intraspecific tree size variation ($\beta = 0.32$), species diversity ($\beta = 0.29$) and interspecific tree size variation ($\beta = 0.28$). Soil fertility had a negative direct effect on interspecific tree size variation ($\beta = -0.31$). Stand quality had a significant positive total effect on aboveground biomass ($\beta = 0.28$), but homegarden size had a significant negative total effect ($\beta = -0.62$), while soil fertility had a non-significant total effect on aboveground biomass. Similar to the no mediation SEM, the partial mediation SEMs had explained almost similar variation in aboveground biomass because species diversity, and intraspecific and interspecific tree size variation had non-significant indirect effects on aboveground biomass via each other. Our results

* Corresponding author.
E-mail address: eskil.mattsson@chalmers.se (E. Mattsson).

http://dx.doi.org/10.1016/j.scitotenv.2017.04.131

strongly suggest that a multilayered tree canopy structure, due to high intraspecific and interspecific tree size variation, increases light capture and efficient utilization of resources among component species, and hence, support the niche complementarity mechanism via plant-plant interactions.

1. Introduction

The relationships between biodiversity and ecosystem functions, particularly aboveground biomass, remain hotly debated in both experimental and natural environments, including forests (Ali et al., 2016a; Isbell et al., 2009; Tilman, 1999; Zhang et al., 2012). These results are important because it suggests that loss of biodiversity could have negative consequences for ecosystem functioning, and the ecosystem services that depend on these (Cardinale et al., 2011; Millennium Ecosystem Assessment, 2005). Yet, most species-structural diversity – aboveground biomass studies in both natural forests and agroforests have focused on individual tree size variation (Ali and Mattsson, 2017; Zhang and Chen, 2015) or variation among species (interspecific) or stand structural diversity (Ali et al., 2016b; Dănescu et al., 2016; Jucker et al., 2016; Poorter et al., 2015). However, variation in aboveground biomass may be partly attributable to tree size variation within species (intraspecific) because it also helps maintain species diversity (Chu et al., 2009; Clark, 2010; de Bello et al., 2011). Therefore, our understanding whether positive relationship between biodiversity and aboveground biomass is fully, partially or not mediated through effects of species diversity, and intraspecific and interspecific tree size variation in forest ecosystems including agroforests remains unclear.

Intraspecific and interspecific tree size variation have been recognized as critical drivers for maintaining individuals within species, co-occurring species dynamics, overall forest diversity and functionality of forests (e.g., Chesson, 2000; Chu et al., 2009; Clark, 2010; de Bello et al., 2011). However, intraspecific tree size variation has been largely overlooked in the previous studies regarding relationships between tree size variation or stand structural diversity and aboveground biomass in both natural forests and agroforests. Lack of consideration of intraspecific tree size variation, instead of interspecific and/or individual tree size variation, may result in misleading conclusions regarding the magnitude and patterns of species-structural diversity – aboveground biomass relationships in both natural forests and agroforests (e.g., Ali and Mattsson, 2017; Ali et al., 2016b; Dănescu et al., 2016; Jucker et al., 2016; Poorter et al., 2015; Zhang and Chen, 2015).

Intraspecific and interspecific tree size variation are also theoretically recognized to express their interactions with nearest neighbors (Chesson, 2000; Chu et al., 2009; Clark, 2010), and may promote aboveground light capture due to different tree canopy heights, and hence light resource use efficiency within a community (Yachi and Loreau, 2007). Species complementarity, e.g. niche differentiation and facilitation, are regarded as the mechanisms for the observed positive relationships between species diversity and aboveground biomass in experimental and natural environments, including forests (Loreau et al., 2001; Zhang and Chen, 2015). Therefore, empirical evidence for species complementarity in driving positive relationships between species diversity and aboveground biomass is scarce due to the fact that tree size variation within and among species represent niche differentiation and facilitation within a community (Chesson, 2000; Clark, 2010). However, empirical studies have found that individual tree size inequality linking positive species diversity and aboveground biomass may reduce the strength of direct positive effect of species diversity on aboveground biomass in both natural forests and agroforests (Ali and Mattsson, 2017; Zhang and Chen, 2015). In this context, we first hypothesize that species diversity, and intraspecific and interspecific tree size variation would independently and directly increase aboveground biomass in agroforestry systems, i.e. the no mediation effect of species diversity and tree size variation (Fig. 1a).

Species diversity is important for the maintenance of stand structural diversity or individual tree size variation (Chesson, 2000; Clark, 2010), and may in turn enhance aboveground biomass (Ali et al., 2016b; Zhang and Chen, 2015). In this case, we hypothesize that species diversity would increase intraspecific and interspecific tree size variation, and as a consequence enhance aboveground biomass, i.e. the full mediation effect of species diversity (Fig. 1b). However, it is increasingly evident that species diversity directly and independently enhances aboveground biomass or productivity in natural forests, due to the increased resource utilization among component species (Dănescu et al., 2016; Hooper et al., 2005; Morin et al., 2011; Poorter et al., 2015; Vilà et al., 2007). Consequently, we further hypothesize that species diversity would enhance aboveground biomass through direct and indirect effects via intraspecific and interspecific tree size variation, i.e. the partial mediation effect of species diversity (Fig. 1c). Alternately, stand structural diversity attributes, such as tree height or diameter diversity, individual tree size variation or mean basal area, are critical to species coexistence (Clark, 2010), and in turn impart the positive indirect effect on the aboveground biomass (Ali et al., 2016b; Jucker et al., 2016; Zhang and Chen, 2015). Interestingly, it has recently been shown that direct effects of species diversity on aboveground biomass is becoming more strengthened, when individual tree size variation is not acting as a linking mechanism for positive species diversity – aboveground biomass in natural forests (Zhang and Chen, 2015). Here, we hypothesize that intraspecific and interspecific tree size variation would increase species diversity, and as a result enhance aboveground biomass, i.e. the full mediation effect of tree size variation (Fig. 1d). In addition, we also hypothesize that intraspecific and interspecific tree size variation would enhance aboveground biomass through direct and indirect effects via species diversity, i.e. the partial mediation effect of tree size variation (Fig. 1e).

Studies on biodiversity – aboveground biomass relationships conducted in forests have been suggested to account for the effects of soil nutrients or fertility, biophysical characteristics of a stand, and heterogeneity in sampling plot sizes that may be important in influencing functions in both natural forests and agroforests (Mattsson et al., 2015; Poorter et al., 2015; Schroth et al., 2015; Zhang et al., 2016). For instance, local soil conditions that determine nutrient and water availability, may strongly influence ecosystem functions such as aboveground biomass, productivity and carbon storage, and may affect relationships between biodiversity and ecosystem function through complex plant–soil feedback loops (see Zhang et al., 2016, and references therein). Furthermore, heterogeneity in sampling plot sizes is known to strongly influence plant community structure, species diversity and aboveground biomass or productivity (Chisholm et al., 2013; Lewis et al., 2009; Poorter et al., 2015). Stand quality should also be included when testing multivariate relationships between biodiversity and aboveground biomass because it determines biophysical characteristics of a stand, particularly stand density, which may influence tree size variation, species diversity and aboveground biomass (Ali and Mattsson, 2017; Schroth et al., 2015). Consequently, we tested our proposed hypotheses after accounting for the exogenous or main effects of soil fertility, homegarden size and stand quality on the relationships of aboveground biomass with species diversity and tree size variation (Fig. 1), by using structural equation models (SEM; Malaeb et al., 2000).