



Research Journal of **Forestry**

ISSN 1819-3439



Academic
Journals Inc.

www.academicjournals.com

A Review of Strong Evidence for the Effect of Functional Dominance on Carbon Stocks in Natural Forest Ecosystems

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ABSTRACT

Natural forest ecosystems are very important because of their potential and primary role in carbon (C) sequestration. However, it is not very clear that whether Functional Trait Diversity (FTD) enhances C stocks in them due to the trait values of the most abundant species (the mass ratio effect; measure as a Community Weighted Mean (CWM) and/or the variety of trait values (the niche complementarity effect; measure as a Functional Divergence (FD) within an ecosystem. In this study, I reviewed the most recent, critical, empirical and original research studies about FTD-C stocks relationship to understand the effects of CWM and FD on C stocks in natural forest ecosystems. The results of their studies suggest that strong dominance by tall and conservative species, rather than a set of coexisting species with diverse heights and exploitative nature, results in greatest C stocks in natural forest ecosystems. Thus, functional dominance (CWM effect) rather than FD effect has strong influence on C stocks in natural forest ecosystems. In conclusions, these evidences reflect that presence of dominant species will finally diminish functional divergence. Therefore, further research is needed to include the abiotic and biotic factors of an ecosystem in the conceptual model to critically test the FTD model of C stocks for full understanding.

Key words: Carbon storage, functional diversity, functional dominance, mass ratio hypothesis, natural forests, niche complementarity hypothesis

INTRODUCTION

The relationship between biodiversity and ecosystem functioning has been a subject of discussion for more than three decades (Grime, 1973). According to Diaz *et al.* (2011), plant Functional Trait Diversity (FTD) is the value, range, distribution and relative abundance of the functional traits of organisms that make up an ecosystem. Depending on the process and the associated service, the key components of FTD might be either the trait values of the most abundant species, the variety of trait values found in the community or the trait values of particular individual species which may be rare (Diaz *et al.*, 2011). Thus, two competing ecological hypotheses have emerged to explain the FTD-(carbon) C stocks relationship in natural forest ecosystems. Firstly, the 'mass ratio hypothesis' (Grime, 1998) postulates that the effects of functional traits of individual species are related to their relative abundance and that the most dominant values of plant functional traits will be the main determining factors of the ecosystem C stocks (Diaz *et al.*, 2009). More explicitly, it implies that the Community Weighted Mean (CWM) value of a trait can be used to predict the C stocks of an ecosystem (Vile *et al.*, 2006; Diaz *et al.*, 2007). Secondly, the 'niche complementarity hypothesis' (Tilman *et al.*, 1997) proposes that the co-existence of different functional strategies, presence of functional traits divergence values, such

as stratified mixtures of shade-tolerant and shade-intolerant species in the community (Lavorel and Grigulis, 2012) should lead to equal resource utilization by the plant community as a whole across time and space. The niche complementarity hypothesis motivated the functional trait divergence (FD), which basically represents the variance in trait values, the abundance-weighted variance of traits using a single trait of each species in the community (Mason *et al.*, 2003). This mass ratio hypothesis (Grime, 1998) is analogous to the hypothesis from biodiversity-ecosystem functioning experiments using plant monocultures and mixtures, which hypothesizes that variations in ecosystem productivity are determined by the presence or absence of highly productive species and not by the variety and complementarity of species (Cardinale *et al.*, 2007). The mass ratio and niche-complementarity effects are not necessarily mutually exclusive; both have been shown to operate in natural ecosystems and can have different relative importance in different situations (Potvin and Gotelli, 2008; Diaz *et al.*, 2009; Mouillot *et al.*, 2011). According to Diaz *et al.* (2007) proposed a conceptual and analytical methodology to test them concurrently in situations that not necessarily involve experimental manipulation. This is particularly relevant to naturally established, species-rich woody ecosystems where manipulation according to traditional experimental design rules is often unfeasible or prohibitively expensive.

Most of the evidences for the effect of FTD on ecosystem processes have been derived from experiments on highly simplified ecosystems (Tilman *et al.*, 1997; Thompson *et al.*, 2005; De Deyn *et al.*, 2009; Pakeman *et al.*, 2011; Roscher *et al.*, 2012). Although, this has the advantages of experimental design and control of co-variances, it has the disadvantage of not certainly demonstrating the most important mechanisms operating in real natural ecosystems (Leuschner *et al.*, 2009). In some studies, the species or functional groups have been experimentally removed from initially homogeneous woody communities in the field (Aguiar and Sala, 1994; Diaz *et al.*, 2003; Bret-Harte *et al.*, 2008; Wardle *et al.*, 2008; Urcelay *et al.*, 2009). Further, many studies have been independently tested the effects of different components of FTD, particularly CWM and FD effects, in natural forests and also assessed the trait-specific relationships with C stocks in natural forest ecosystems (Caspersen and Pacala, 2001; Delagrange *et al.*, 2008; Jonsson and Wardle, 2010; Ruiz-Jaen and Potvin, 2011; Wardle *et al.*, 2012). However, empirical studies focusing on the comparison of CWM (the mass ratio hypothesis) and FD (the niche complementarity) effects on C stocks in the naturally established forest ecosystems are still very scarce (Conti and Diaz, 2013; Cavanaugh *et al.*, 2014; Finegan *et al.*, 2015). Thus, our understanding about how functional dominance *versus* divergence affects the C stocks in natural forest ecosystems remains poorly understood.

In this study, I reviewed the most recent, critical, empirical and original research studies focusing on both mass ratio and niche complementarity hypotheses to investigate the relationship between FTD and C stocks in natural forest ecosystems. The aims of this study are to highlight the role of CWM and FD on C stocks in natural forest ecosystems and to recommend future research based on the uncompleted current state of knowledge.

ROLE OF THE PLANT ECONOMICS SPECTRUM IN FTD-CARBON STOCKS RELATIONSHIP

The leaf economics spectrum ranges from 'exploitative' plants with fast nutrient acquisition and turnover, associated with thinner, nitrogen-rich leaves and fast growth (e.g., high leaf nitrogen concentration-LNC, high specific leaf area-SLA) to 'conservative' plants with denser, nutrient-poor leaves and slower growth (e.g., high leaf dry matter content-LDMC, low LNC; Wright *et al.*, 2004).

Finegan *et al.* (2015) observed the strong relationship of leaf economics spectrum (CWM of leaf traits particularly SLA) to productivity including, initial aboveground biomass (thus, above ground C stock), biomass of survivors and recruits in tropical forest ecosystems. This implies that communities dominated by exploitative plants are associated with overall faster nutrient turnover and the opposite are true for communities dominated by conservative plants (Lavorel and Grigulis, 2012). This scaling effect from the leaf economics spectrum to C stocks was, however, not observed either along an altitudinal gradient in semi-arid forest ecosystems in Chaco (Conti and Diaz, 2013), where instead CWM of stem wood density was better predictors of C stocks. In contrast, Cavanaugh *et al.* (2014) found that the CWM of stem wood density appeared to be unimportant as a factor explaining aboveground C stock in tropical forest ecosystems at global scale, argues against their hypothesis that aboveground C stock is generally related to the dominance of trees with either high or low wood densities (Stegen *et al.*, 2009). These above results provide support for the general hypothesis that plant economics may not only be reflected in leaves, but also in stems at species (Freschet *et al.*, 2010) and at community level (Perez-Ramos *et al.*, 2012). However, most of the studies focusing on the relationship between FTD and C stocks did not consider the whole plant coordination and root traits are particularly ignored due to technical difficulties and are often substituted by measurement of leaf functional traits (Conti and Diaz, 2013; Cavanaugh *et al.*, 2014; Finegan *et al.*, 2015). It is recommended to include root traits, in addition to leaf and stem traits, in further studies concerning FTD and C stocks in natural forest ecosystems (Orwin *et al.*, 2010; Grigulis *et al.*, 2013). Because, root traits have been recognized to have more direct ecosystem effects (Butterfield and Suding, 2013) and may not always be well associated with leaf traits (Orwin *et al.*, 2010; Fortunel *et al.*, 2012). Thus, our understanding about the role of whole plant traits coordination in the relationship between FTD and C stocks remains poorly understood. Thus, urgent researches need to cover this knowledge gap in the natural forest ecosystems.

STRONG EVIDENCES FOR THE MASS RATIO HYPOTHESIS AND POOR EVIDENCES FOR THE NICHE COMPLEMENTARITY HYPOTHESIS

Several earlier studies conducted in different terrestrial ecosystems have suggested that plant functional trait effects may primarily be attributed to the mass ratio hypothesis (CWM effects) rather than to divergence effects (FD effects) (Mokany *et al.*, 2008; Laughlin, 2011; Lavorel *et al.*, 2011), sometimes due to correlation between these two FTD indices (Dias *et al.*, 2013). Still, most recent studies have also strongly supported the mass ratio hypothesis, while poorly or no support for the niche complementarity hypothesis regarding FTD-C stocks relationship in natural forest ecosystems. However, some non-significant and negative FD effects were also retained in the final models of C stocks (Conti and Diaz, 2013). These negative FD and positive CWM effects reported for initial production suggest that strong dominance by tall species, rather than a set of coexisting species with diverse heights, results in greatest C stocks in natural forest ecosystems (Conti and Diaz, 2013; Finegan *et al.*, 2015). Thus, these tall species may also have denser wood and greater below ground production and hence make a greater contribution to C stocks. However, Cavanaugh *et al.* (2014) conducted a global scale study in natural tropical forests and found a positive relationship between CWM of maximum diameter and C stocks, suggests that characteristics of the dominant trees (specifically their maximum potential diameter) results greatest aboveground C stock in mature forests, strongly supported the mass ratio hypothesis. Cavanaugh *et al.* (2014) and Finegan *et al.* (2015) did not find a significant relationship between FD and C stock which is in disagreement with the niche complementarity hypothesis (Tilman *et al.*, 1997). Although, Cavanaugh *et al.* (2014) found a positive association between

taxonomic diversity and C stocks, supports partly the niche complementarity hypothesis. However, functional traits are most important to complementary resource allocation (Petchey and Gaston, 2006). These above results may be happened due to the ignorance of abiotic and biotic factors of the ecosystems in their conceptual model.

CONCLUSION

It is concluded that functional traits of the dominant species have strong influence on C stocks in natural forest ecosystem. In addition, the increasing probability at high productivity levels that one or a few highly competitive species out-compete other species could also counteract resource-use complementarity and finally diminish functional divergence (Schumacher and Roscher, 2009). Although many studies have supported the mass ratio hypothesis, the deficiencies remain to fully understand the FTD-C stocks relationship in the natural forest ecosystems. Therefore, it is worth important for future studies to consider the mechanism of intra- and/or inter-specific competition and their associations with ecosystem productivity in natural forests. In addition, it is also much important to consider the whole plant coordination in the future studies of FTD-C stocks in natural forest ecosystems. Thus, an urgent research is needed to test one interactive conceptual model, including CWM and FD of traits, soil factors, topography, inequality of stand, species diversity and competition, on C stocks in natural forest ecosystems.

ACKNOWLEDGMENTS

The author is thankful to China Scholarship Council (CSC) and Pakistan Higher Education Commission (HEC) for providing full financial support to conduct his study at East China Normal University, Shanghai, China.

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