

Relationships between biodiversity and carbon stocks in forest ecosystems: a systematic literature review

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Abstract: A systematic literature review was conducted to explore the relationships between multiple measures of biodiversity (e.g. species diversity, functional divergence and dominance) and carbon (C) stocks (both aboveground and soil organic) in different forest ecosystems. A total of 47 studies, searched in Web of Science or Knowledge, were selected based on different biodiversity indices, strength of the datasets and particularly focusing on C stocks. The majority of relationships between species diversity or richness and C stocks were positive, while only few were negative. The niche complementarity and the mass ratio hypotheses are the two major hypotheses for explaining the effect of functional diversity on C stocks. These two hypotheses did not contradict each other but reflect the two different sides of functional trait attribute i.e., dominance and divergence. The majority of studies suggested that strong dominance by tall and conservative species, rather than a set of coexisting species with diverse heights and acquisitive role, results in more C stocks in various forest ecosystems. Thus, most of the studies supported mass ratio hypothesis instead of the niche complementarity hypothesis in terms of increasing C stocks in forest ecosystems. We concluded that experimental works in other forest ecosystems have shown that each measure of biodiversity often increases C stocks, although the extent to which direct causal relationships exist between biodiversity and C stocks in subtropical forests are still uncertain. Thus, a little is understood how multiple measures of biodiversity affect C stocks, when also considering the effects of biotic and abiotic components of an ecosystem.

Key words: Carbon stocks, functional diversity, mass ratio hypothesis, niche complementarity hypothesis, stand structural diversity.

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Introduction

Carbon (C) is continuously removed from the atmosphere by forest ecosystem processes and stored both in vegetation and soils (e.g. McGuire *et al.* 2001). If C stocks of ecosystems increase, the C

content of the atmosphere is reduced. On the other hand, if the C stocks in ecosystems were to reduce, the increase rate of carbon dioxide (CO₂) in the atmosphere would be much faster than currently observed (Reich 2011). Therefore, global forests are very diverse and provide a range of ecosystem

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services such as C sequestration, flood and landslide protection, biodiversity preservations, aesthetic and health benefits (Pan *et al.* 2013). Forest is usually defined by the presence of trees and absence of non-forest land use, even though trees are also numerous outside forests in savannas, pasture lands, and in suburban areas and green city centers (Nowak & Greenfield 2012). According to FAO (2001), forest refers to land with a tree canopy cover of more than 10% and area of more than 0.5 ha, but determination is focusing on the presence of trees and the absence of other predominant land uses. On the other hand, wooded land refers to a land that has either a crown cover (or equivalent stocking level) of 5 to 10% of trees able to reach a height of 5 m at maturity; or a crown cover (or equivalent stocking level) of more than 10% of trees not able to reach a height of 5 m at maturity; or with shrub or bush cover of more than 10%. The term “forest” specifically excludes non-forest land use such as stands of trees established primarily for agricultural production, for example fruit tree plantations and agroforestry systems (FAO 2001). Hence, forest trees are recognized as very important in the global C cycling, because of the amount of C stored in plant biomass globally exceeds that of atmospheric CO₂, and nearly 90% of the plant biomass C is stored in tree biomass (Mooney *et al.* 2001).

Forests are thus the worldwide fundamental C pool and sink sequestering approximate 47% of terrestrial C (Table 1, Dixon *et al.* 1994). The CO₂ sequestration among forests depends on forest type, dominant tree species and stand age (Huy & Anh 2008). Furthermore, the role of that biodiversity play in shaping ecosystem functioning has become concern in ecology (Loreau *et al.* 2001). For developing the best ecological plans to protect biodiversity, maintain ecosystem productivity and mitigate the effects of global warming, the relationships between species diversity and ecosystem productivity and thus C stocks have received particular emphasis in recent decades (Bosworth *et al.* 2008; Con *et al.* 2013; Firn *et al.* 2007; Kirby & Potvin 2007; Lei *et al.* 2009; Liang *et al.* 2007; Mittelbach *et al.* 2001; Vilà *et al.* 2003). However, in the forested ecosystems, discrepancies among studies remain unresolved. This highlights the need to precisely determine the amount of C stored in each specific forest ecosystem.

Can plant functional and structural diversity be a driver for ecosystem C stocks, and which plant functional traits should be the most relevant? This extensive question has attracted

Table 1. Contributions of different biomes in global C stocks. Boreal forests contribute more total C stocks than any other terrestrial ecosystem (23% of total terrestrial C stocks), tropical and subtropical forests account for 17% while temperate forests account for 7% (Dixon *et al.* 1994).

| Biome | Area (10 ⁹ ha) | Vegetation | Soil | Total | Percentage |
|----------------------------------|------------------------------|------------|------|-------|------------|
| Boreal forests | 1.37 | 88 | 471 | 559 | 22.57 |
| Tropical and subtropical forests | 1.76 | 212 | 216 | 428 | 17.28 |
| Tropical savannas | 2.25 | 66 | 264 | 330 | 13.32 |
| Temperate grasslands | 1.25 | 9 | 295 | 304 | 12.27 |
| Wetlands | 0.35 | 15 | 225 | 240 | 9.69 |
| Deserts and semi-deserts | 4.55 | 8 | 191 | 199 | 8.03 |
| Temperate forests | 1.04 | 59 | 100 | 159 | 6.42 |
| Croplands | 1.60 | 3 | 128 | 131 | 5.29 |
| Tundra | 0.95 | 6 | 121 | 127 | 5.13 |
| Total | | 466 | 2011 | 2477 | 100 |
| | 15.12 | | | | |

Note: Total C stocks = 2477 Gt, 1 gigatonne (Gt) = 1 billion tonnes. Source: (Dixon *et al.* 1994).

broad interest with respect to both hypothetical and managerial motivations. This is the case as these functional traits should be measured by considering the main organs of the plants i.e. stem, leaf, branch or twig and root, in order to explore the association of biodiversity-C stocks, on the basis of different functional traits. It is well understood that during the process of photosynthesis, the atmospheric CO₂ is utilized by the leaves for the production of food in the form of glucose. Later on, it is diverted to other tree components for storage by getting increase in their biomass through growth (Matthews *et al.* 2000; Negi *et al.* 2003). Therefore, the higher biomass is associated with larger divergence of height (Butterfield & Suding 2013) and branches, resulting in complex stand structure, yield more production and its C content clearly drive the total amount of C stocks. Functional traits related with plant tissue quality influence the residence of

living tissues and therefore influence SOCS (De Deyn *et al.* 2008; Wardle *et al.* 2004). In particular, there is trade-off among functional attributes, called the acquisition versus conservation axis (Díaz *et al.* 2004) or the leaf economic spectrum (Wright *et al.* 2004), is strongly driven by a set of coordinated leaf traits. The leaf economics spectrum ranges from ‘exploitative’ plants with fast nutrient acquisition and turnover (e.g. high specific leaf area-SLA, high leaf nitrogen concentration-LNC), to ‘conservative’ plants with denser, nutrient-poor leaves and slower growth (e.g. high leaf dry matter content-LDMC, low LNC) i.e. conservation of resources and slow decomposition (e.g. Díaz *et al.* 2004; Poorter *et al.* 2009; Wright *et al.* 2004). At the ecosystem level, prevailing acquisitive syndromes should be conducive to higher C fluxes, whereas prevailing conservative syndromes should be conducive to higher C stocks (De Deyn *et al.* 2008, Díaz *et al.* 2006; Wardle *et al.* 2004).

The functional changes of tree basal diameter and height have shown to directly influence the amount of ACS and SOCS, thus incorporating into the soil as litters at senescence (De Deyn *et al.* 2008; Lavorel & Grigulis 2012). In addition, large trees are expected to shed more biomass in the form of leaf and woody litter per unit ground area and thus contribute directly to C stocks in the standing litter and in the organic soil (Lavorel & Grigulis 2012). Therefore, functional traits with respect to plant tissue quality, such as leaf nutrient concentration and leaf area displayed per unit C, influence the residence time of both living tissues and litter and eventually influence SOCS (Aerts & Chapin 2000; De Deyn *et al.* 2008).

This systematic literature review provides an overview of the current state of knowledge regarding relationships between multiple measures of biodiversity indices and C stocks in various forest ecosystems. Based on reviews of relevant, critical and recent (restricted to December, 2014) literatures, this study aims at clarifying the current state of knowledge, research knowledge gap in different forest ecosystems, mechanisms regarding biodiversity-C stocks relationships in forest ecosystems. Specifically, we focused on the species diversity and functional diversity i.e. functional dominance and divergence, and evidence of their effect on C stocks (ACS or SOCS) in different forest ecosystems. We also explored the direction (positive, negative or neutral) of this effect in order to understand the

complex nature of the biodiversity-C stocks relationships and explore future research challenges. In addition, we were also interested in providing an overview of the scarce studies conducted in subtropical forests because they were particularly ignored (e.g. Cardinale *et al.* 2006). However, subtropical forests contain high biodiversity value and have significant role in the mitigation of current climatic change (Yu *et al.* 2014).

Basic ecological concepts

Concept of biodiversity in forest ecology

According to Díaz *et al.* (2006), biodiversity is the number, abundance, composition, spatial distribution, and interactions of genotypes, populations, species, functional types and traits and landscape units in a given system. In ecology, the literature on diversity is infinite but three measures of diversity are well-known including species richness, Gini-Simpson diversity, and Shannon-Wiener’s diversity index. Species richness, a simple calculation of the species numbers, is easy but it ignores frequency of species. Shannon-Wiener’s diversity index was a measure of entropy in the beginning but afterward applied to information theory (Shannon 1948; Shannon & Weaver 1949). The Gini-Simpson diversity index (Simpson 1949) had in fact been used formerly to measure economic discrimination. All the above three ecological diversity indices are closely linked which can be derived from the same one-parameter family of diversity indices (Keylock 2005; Patil & Tailie 1979). Shannon-Wiener’s index for stand structural diversities (tree species, size and height diversity) reflects both species evenness (E) and richness (S) (Magurran 1988), without supporting either dominant or rare species while Simpson’s index favour dominant species.

In addition, functional diversity is recognized to treat all species as ecologically non-independent and may therefore provide enough information about the relationships between biodiversity and ecosystem function such as productivity (Tilman *et al.* 1997). Two components of plant functional diversity are commonly used to test the strength of relationship between biodiversity and ecosystem C stocks (Fig. 1). First, community weighted trait means (CWM), as an indicator for functional dominance, represents the expected functional trait value of a specific community (Díaz *et al.* 2007). Secondly, functional divergence of a single-

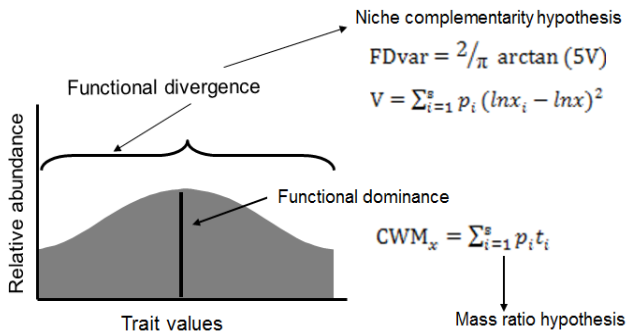


Fig. 1. Conceptual diagram for functional diversity components i.e. functional dominance and divergence. The functional dominance support mass ratio hypothesis while functional divergence support niche complementarity hypothesis.

trait, basically represents the variance in a trait value by weighting the abundance of each species in the community (Mason *et al.* 2003).

The summary of procedures for calculations, and short descriptions of multiple measures of biodiversity indices are shown in Table S1.

Humans and ecosystem services

Anthropogenic change threatens biodiversity worldwide and increased the accelerating rate of species extinction up to one thousand times the background rate by modifying the environment (Andelman & Willig 2003; Carney *et al.* 2004; Millennium Assessment 2005; Sala *et al.* 2000). According to the International Union for Nature Conservation (IUCN 2009), Red List of Threatened Species, 36% of 47,677 evaluated species are endangered with extinction including 70% of the plant species evaluated. Humans are dependent on ecosystems for the services they offer; however, the capability for ecosystems to offer these services depends on how humans treat them. And, while it is plausible that ecosystem services are reliant on biota, there is incomplete knowledge in how exactly ecosystem services are reacting to the current trend of biodiversity loss. In an attempt to fill this gap in knowledge, ecologists have commenced a motivated research effort to quantify how biodiversity losses affect ecosystems. An important goal in ecology is to understand ecosystem structure through quantification of biodiversity and ecosystem processes and determining the relationships between them (Keddy 2005; Hooper *et al.* 2005).

Concept of biodiversity and ecosystem functioning (BEF)

In the past 30 years, interest has increased dramatically in determining the BEF relationships. One of the most commonly studied relationships is that between species richness and productivity, or its surrogates (see, Mittelbach *et al.* 2001; Waide *et al.* 1999 for additional references). However, most productivity-species richness studies have been conducted in grasslands (Caspersen & Pacala 2001; Chalcraft *et al.* 2009; Creed *et al.* 2009; Hector *et al.* 1999; Tilman *et al.* 1996), and only a few in forests (Lei *et al.* 2009; Liang *et al.* 2007). The associations between tree species diversity and ecosystem productivity have been reported to be either positive (Balvanera *et al.* 2006; Erskine *et al.* 2006; Hector *et al.* 1999; Tilman *et al.* 1996, Whittaker & Heegaard 2003), negative (Huston 1980; Firn *et al.* 2007), or non-significant (Vilà *et al.* 2003). Early experiments conducted in grasslands showed mostly a decrease in plant productivity with a decline in plant species richness (e.g. Balvanera *et al.* 2006; Erskine *et al.* 2006; Hector *et al.* 1999; Naeem *et al.* 1994, Tilman *et al.* 1996, Whittaker & Heegaard 2003).

Much of the discussion over the mechanisms behind observed BEF relationships has focused on whether species diversity effects are driven by niche partitioning and facilitation (i.e. the complementarity effect, Tilman *et al.* 1997) or by the selection of one or more highly productive species such as the selection effect (Cardinale *et al.* 2012). The niche complementarity hypothesis postulates that a diverse array of species has a greater divergence of functional traits and can thus better utilize limiting resources, thus increasing total ecosystem functioning, than a less diverse community. The complementarity effect is the increase in relative productivity among species in a mixture compared with the productivity of the species grown in monocultures due to positive interactions among species (i.e. facilitation and partitioning of resources, e.g. Naeem *et al.* 1994, Tilman *et al.* 1996). The mass ratio (selection effect) hypothesis states that most dominant species or traits drive ecosystem functioning and that positive BEF relationships arise simply because diverse communities are more likely to include high functioning species and traits. A better understanding of how functional divergence and dominance affect ecosystem function would

help direct preservation and restoration plans for exploited ecosystems.

Positive relationships among species, rather than the existence of a highly dominant species, mostly determine the effect of diversity on plant productivity (Cardinale *et al.* 2007). In a meta-analysis of 44 separate BEF experiments (39 in terrestrial grassland, two each in tundra and bryophyte, and one in estuarine), Cardinale *et al.* (2007) observed that plant productivity increased with diversity because of the complementarity effect in most experiments and that the effect increased over time. Complementarity occurs when species either facilitate the growth and insistence of other species (e.g. legumes fixing nitrogen, Hooper & Dukes 2004) or partition the utilization of resources either temporally, spatially or chemically (e.g. temporal differences in nitrogen use, Hector 1998). Specific experiments testing for facilitation and resource (e.g. nitrogen) partitioning are necessary to determine the mechanism resulting in a complementarity effect (e.g. von Felten *et al.* 2009), and so far quite little is known about specific mechanisms motivating the effects of biodiversity on C stocks. The current consensus among ecologists is that the loss of biodiversity alters ecosystem functions (Hooper *et al.* 2005). Due to logistic ease, most BEF research has been on productivity and nutrient retention in experimental grassland ecosystems, however the applicability of these results to forest ecosystems and non-experimental settings is questionable (Loreau *et al.* 2001). In a meta-analysis of 449 BEF studies, biodiversity effects were shown to vary among ecosystem types (Balvanera *et al.* 2006). However, certain ecosystems are very scarce in the literature (e.g. subtropical forest ecosystems; Cardinale *et al.* 2006; Table 2).

Literature search and data collection

In order to review and collect existing research on the relationships between biodiversity and C stocks in forest ecosystems, a literature search was conducted between August 2013 and December 2014 using Web of Science or Web of Knowledge. The main objective of focusing on peer-reviewed academic literature was to find the best current state of knowledge reported by the scientific community. A systematic methodology was implemented in order to confirm that a critical method was applied to each type of forest ecosystem as well as to each biodiversity index (see conceptual model in Fig. 2). The method consisted

Table 2. Representations of various biomes in biodiversity–ecosystem functioning literature. “Other terrestrial ecosystems” refers to the category containing emergent tropical and subtropical forests studies. The studies conducted in each biome are presented through percentage. Modified statistics from Cardinale *et al.* (2006).

| Biome | Percentage |
|------------------------------|------------|
| Temperate grasslands | 34 |
| Lakes | 18 |
| Streams | 15 |
| Temperate forests | 8 |
| Coastal | 8 |
| Estuarine | 8 |
| Agricultural lands | 6 |
| Other freshwater ecosystems | 2 |
| Other terrestrial ecosystems | 1 |
| Total | 100 |

of four steps, i.e. (1) the generation of keywords, (2) a systematic search of literature, (3) collection of the data or highlight of the key findings, and (4) Interpretation of the review highlights.

Keywords were generated based on the “basic ecological concepts” (see section 2)” which showed that ‘biodiversity’ is a relatively broad term and, hence, only using this term in a literature search is likely to miss relevant papers on forest ecosystems. Thus, keywords specific to biodiversity indices such as (tree) species diversity or richness, tree size or height diversity, (plant) functional (trait) diversity and functional (trait) dominance, were selected, accompanied by the names of different types of forest ecosystems, e.g. tropical, subtropical, temperate, alpine or subalpine and boreal ecosystems. We included synonyms (i.e. C storage, C sequestration, forest biomass or aboveground biomass, soil organic C and ecosystem C stocks) to C stocks in the search terms to collect more relevant papers. In addition, we also used relationship-related terms i.e. negative or positive (if necessary) to enable negative as well as positive effects of biodiversity on C stocks, when enormous quantities of papers were found for the initial search terms.

The objective was to find more relevant papers for the relationships between biodiversity and C stocks in order to explore a wide range of relationships, with emphasized on forest ecosystems. We also collected the papers by searching the reference lists of relevant papers for secondary references, and through searching for papers that have cited the relevant papers. In

total, 62 critical papers were found, where only few studies have related functional diversity or dominance to C stocks while most of the studies have been focused on species diversity or richness. Out of the different types of forest ecosystems, only one critical study was conducted in subtropical forests while most of the studies have been conducted in other forest ecosystems, despite of studies focusing on global datasets (also see Cardinale *et al.* 2006 and Table 2 for more information).

The main findings or results from 62 research articles were consolidated, where 27 articles have particularly focused on C stocks or biomass while the remaining articles have included biomass or C stock as a component of ecosystem functioning or measure for productivity. The parameters collected from articles covering: (1) the ecosystem C stocks or biomass; (2) biodiversity indices; (3) ecosystem types; (4) study locations, and (5) directions of relationships. The final parameters collected from searched articles included species attributes (presence or absence of a specific species type, species abundance, species richness, Shannon's or Simpson's species diversity, species size and height, growth rate, mortality rate, and survivor rate); functional group attributes (functional divergence or richness, and functional dominance); and ecosystem C stocks or biomass (aboveground, belowground, productivity measured in biomass, and soil organic C or belowground biomass). The type of ecosystems included tropical, subtropical, temperate, alpine or subalpine, and boreal ecosystems, while grassland ecosystems were also considered for comparison purpose. The study locations included Asia, Africa and America. The direction of each relationship between the biodiversity index and the ecosystem C stocks was also highlighted as being predominantly positive, negative or neutral. Finally, 47 papers were included in the literature review based on the following three main points: (1) if the similar findings were found for each biodiversity index with C stocks in the same type of ecosystem, then only two or three critical studies conducted in different study locations were referenced to shortened the references list; (2) studies were selected according to the strength of the dataset along with the advancement in applied statistical analyses; and (3) the studies that have mainly focused on C stocks or biomass in relationships to the important biodiversity indices.

It was worth to mention here that this study mainly focused to highlight the current state of

knowledge through literature review, instead of focusing on any statistical or data analysis. However, we had displayed some modified statistics collected from searched papers (references have been cited properly).

Review highlights and discussion

Relationships between species diversity and C stocks in different forest ecosystems

Few studies have looked at the relationship between biodiversity and C stocks in forest ecosystems (Caspersen & Pacala 2001, Creed *et al.* 2009), perhaps because of the difficulty in using biomass as a surrogate for productivity in long-lived trees (Vance-Chalcraft *et al.* 2010).

Furthermore, these relationships in the subtropical forests are relatively scarce in the literature. According to Cardinale *et al.* (2006), 34% of BEF studies have been conducted in the temperate grasslands, 18% in lakes, 15% in streams, 8% in each of estuarine and coastal, 6% in agricultural lands, and 2% in other fresh water ecosystems, while 8% in temperate forests but only 1% of BEF study has been conducted in other terrestrial ecosystems including tropical and subtropical forests (Table 2). Out of that 1% research, most of the studies have been conducted

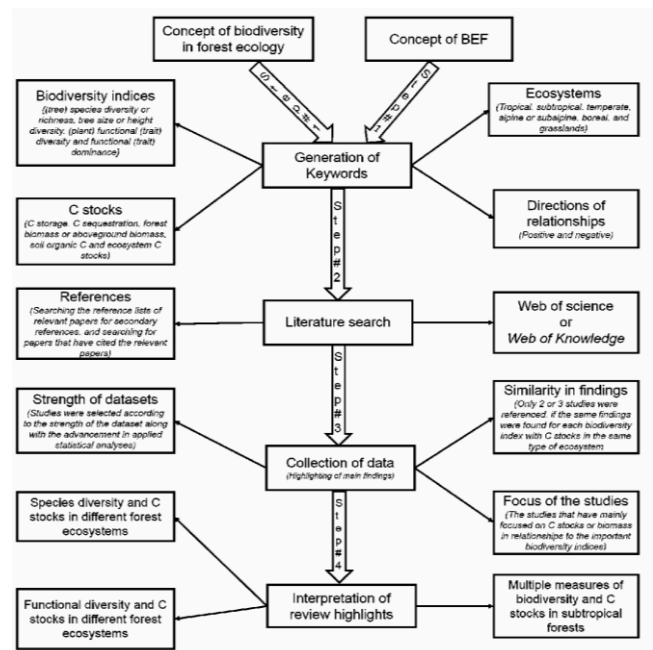


Fig. 2. A conceptual framework for the systematic literature review on the relationships between biodiversity and C stocks in different forest ecosystems.

in tropical and other forests ecosystems (excluding temperate forests) while subtropical forests were particularly ignored.

The existing research conducted in other forest ecosystems showed different relationships between tree species diversity and C stocks. For example, significant positive relationships between them was observed in dry tropical forests of India (Sagar & Singh 2006), deciduous forests of north America (Houle 2007) and agro-ecosystems of in south western Uganda (Nakakaawa *et al.* 2009). On the other hand, Szwagrzyk & Gazda (2007) reported that negative relationship exists between AGB and tree species diversity in natural temperate forests of Central Europe and the same conclusion was found for *Quercus* communities in the transition zone of subtropical and warm temperate in northwest China (An-ning *et al.* 2008). Another case is a meta-analysis by Phillips *et al.* (1994) showing that there was a positive relationship between forest dynamic and tree species richness in tropical rain forests. Furthermore, Bunker *et al.* (2005) reported that a simulation of 18 possible extinction scenarios using the data from a 50 ha tropical forest plot shows that C stocks in tropical forest depends on species composition. However, Chen (2006) reported a positive relationship between tree species diversity and SOCS in the top 30 cm soil layer in an old-growth forest of northeast China, but Jonsson & Wardle (2009) reported that plant diversity weakly affects belowground C stocks in boreal forest ecosystems. On the other hand, Zhang *et al.* (2011) found no significant relationship between plant diversity and SOCS in the top 30 cm soil in a subalpine coniferous forest in southwest China. Thus, this variability may probably be explained by the confounding effects resulting from other stand variables such as height, size, age, site productivity and stand density that significantly influence ecosystem productivity (Lei *et al.* 2009; Liang *et al.* 2007) and might also affect ecosystem C stocks differently.

In addition to species diversity, forest C stocks are also affected by many other stand variables, such as tree size and stand characteristics (Buongiorno *et al.* 1994; Lindenmayer & Franklin 1997; Sullivan *et al.* 2001; Upadhaya *et al.* 2015; Varga *et al.* 2005). Stand structural diversity has been observed to influence forest productivity (Lei *et al.* 2009; Liang *et al.* 2007) and ecosystem C stock (Wang *et al.* 2011). Also, stand age, site productivity and stand density affect stand growth and stand structural diversity (Lei *et al.* 2009;

Liang *et al.* 2007). Hence, only species diversity is not enough to explain variations in forest C stock because tree diameter and height are key elements for shaping stand structural diversity that has been documented to significantly affect forest C stocks or biomass (Baishya *et al.* 2009; Lexerød & Eid 2006). In our knowledge, only one study focused on the relationships between stand structural diversity (species, size and height diversity) and ACS. Such as, Wang *et al.* (2011) found that increased stand structural diversity enhances ACS in spruce-dominated forest stands in New Brunswick, Canada. In addition, Con *et al.* (2013) used the multiple measures of biodiversity (species richness, Shannon diversity index, and evenness) and of structure–species diversity (biomass–species and abundance–biomass–species diversities) to determine the patterns and strengths of relationship between each biodiversity measure and AGB in tropical forests of Vietnam. Thus, relationships between measures of biodiversity and AGB were generally weaker than that between measures of structure–species diversity and AGB. Hence Con *et al.* (2013) finding indicates that structure–species diversity is a sound index representing the role of tropical forest in storing biomass and may suggest that uneven-aged and multistoried plantations should be encouraged for C stocks.

Thus manipulating stand structural diversity may be a useful tool for maintaining ecosystem biodiversity and productivity (Varga *et al.* 2005). Currently, how do stand structural diversity indices affect ACS and particularly SOCS when controlling for stand age, site productivity and stand density, in various forest ecosystems, still remains unclear.

Relationships between functional diversity and C stocks in different forest ecosystems

Recent studies that focusses on biodiversity have begun to include the concept of functional diversity (Butterfield & Suding 2013; Conti & Díaz 2013; Finegan *et al.* 2015), which measures the range, value, and distribution of functional traits of organisms in a community ecosystem (Tilman *et al.* 1997). It is becoming increasingly accepted that biodiversity components of plant community, i.e. the species identity, abundance and divergence of functional traits, strongly affect ecosystem productivity, functioning, litter decomposition and soil nutrients dynamics (De Deyn *et al.* 2008; Díaz *et al.* 2004; Hooper *et al.* 2005; Mouillot *et al.* 2005;

Naeem & Wright 2003; Wardle *et al.* 2004; Wardle *et al.* 2012). But unfortunately, field tests based on empirical data examining which components of functional diversity best predict ecosystem C stocks in the forested ecosystems are relatively scarce in the literature. Currently, only few studies have tested the assumption of mass ratio and niche complementarity hypotheses, in terms of linkage between functional diversity and C stocks (Butterfield & Suding 2013; Conti & Díaz 2013; Finegan *et al.* 2015).

Recently, Finegan *et al.* (2015) demonstrated the strong association of the leaf economics spectrum (CWM of leaf traits particularly SLA) to ACS, including initial AGB, biomass of survivors and recruits in tropical forest ecosystems: communities dominated by exploitative plants were associated with overall faster nutrient turnover – and the opposite was true for communities dominated by conservative plants (Lavorel & 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 & Díaz 2013), where instead CWM of stem wood density was better predictors of C stocks. Recently, Finegan *et al.* (2015) and Conti & Díaz (2013) suggested 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. Comparatively, Butterfield & Suding (2013) reported that functional divergence of height among rangeland herbs links with higher production in Californian rangeland, supporting niche-complementarity hypothesis. Jonsson & Wardle (2009) and Wardle *et al.* (2012) also given more support to mass ratio hypothesis that communities dominated by acquisitive trait values showed lower below-ground C storage than communities dominated by more conservative trait values in boreal forests. In natural moist seasonal tropical forests, Ruiz-Jaen & Potvin (2011) reported that C stocks associated positively with plant height and leaf mass per area (the inverse of SLA) and negatively with the variety of values of these traits values, giving more support to mass-ratio hypothesis while in neighboring plantations, in contrast, they found a negative association of C stocks with plant height and leaf mass per area and a non-significant association with variety of values of these traits values, giving more weight to niche-complementarity hypothesis.

Moreover, Cavanaugh *et al.* (2014) conducted a global scale study, in which they partly supported both hypotheses on the basis of functional dominance and taxonomic diversity (genus richness and Shannon diversity). However, they did not find a significant relationship between functional diversity and ACS. In their study, the functional diversity components were calculated using the maximum diameter of stems and stem wood density only, but did not include leaf economics. It has been recognized that leaf economics link plant resource use strategy and plant C economics functionally (Lavorel & Grigulis 2012). This thus might be one of the reasons why functional diversity did not correlate to ACS in their study. Thus, it is important to consider both the mass ratio hypothesis and the complementarity hypothesis when functional diversity-C stocks associations are examined.

These positive relationships appears to be determined both by individual, dominant species and some form of complementarity among species, reflecting assumptions from recent meta-analyses of manipulative studies (Cardinale *et al.* 2011; Cardinale *et al.* 2012). Most of the other observational studies that have related biodiversity to biomass or productivity in forests have been conducted in relatively species-poor temperate and boreal forest ecosystem (Caspersen & Pacala 2001; Vilà *et al.* 2007). Much less is known about these relationships in highly diverse tropical and particularly subtropical natural forests.

Based on the assumptions of the mass ratio hypothesis (Grime 1998), functional strategies of the dominant species have overwhelming influence on ecosystem C stocks. The increasing probability at high productivity levels that one or a few highly competitive species out-compete other species can counteract resource-use complementarity and finally diminish functional divergence (Schumacher & Roscher 2009; also see the review (Ali 2015) for additional references). Unfortunately, very few studies have compared the explanatory power of both hypotheses concurrently with respect to relationships between functional diversity components and each of ACS and SOCS within forest ecosystems (Ali 2015).

Relationships between multiple measures of biodiversity and C stocks in subtropical forests

Unfortunately the majority of biodiversity-C stocks studies are concentrated in tropical or

temperate forests with a lack of studies in subtropical forests. The only one critical study that we found was conducted Vance-Chalcraft *et al.* (2010), which determined the relationships between each of five the measures of biodiversity index (i.e., species richness, Simpson's diversity, Simpson's evenness, rarity, and dominance) and AGB in subtropical forests of Puerto Rico. Vance-Chalcraft *et al.* (2010) found that unimodal species richness–AGB relationships are predominant in subtropical forests, except at the most mature stands. However, Vance-Chalcraft *et al.* (2010) didn't included the effects of stand maturity (age), size (diameter), height and functional traits in their study. This thus might be one of the reasons of why biodiversity indices correlate differently with AGB in different stands of the studied forests. In conclusion, the big knowledge gap of how functional dominance (mass ratio hypothesis) and divergence (niche complementarity hypothesis) affect the biodiversity-C stocks relationship in subtropical forests still exists.

Conclusions and recommendations for future research

Recently interest has increased dramatically in determining the biodiversity-C stocks relationships in forest ecosystems but still discrepancies among studies remain unresolved. This section highlights some of the relevant knowledge gaps in our understanding. In addition, direct relationships between biodiversity and C stocks in subtropical forests are poorly understood. The nature of these forests, in particular the very high diversity and the exceptionally long lifespan of the trees, makes it impractical to establish experimental plots to represent natural forests. Observational studies are possible in a way that deals reasonably with all of the co-varying environmental variables.

The accurate quantification of AGB in forest ecosystems, although still a challenge is important for national carbon accounting, Reducing Emissions from Deforestation and Forest Degradation (REDD+) project payments, sustainable forest management and strategic policy-making (Ali *et al.* 2015; Chave *et al.* 2005; Timothy *et al.* 2016). In forest ecosystems, shrubs and small trees (DBH < 5 cm) play important roles for structuring AGB (Ali *et al.* 2015). Although there are well-developed generalized allometric equations for big trees (DBH > 5 cm, e.g. Brown *et al.* 1989, Chave *et al.* 2005), those equations are

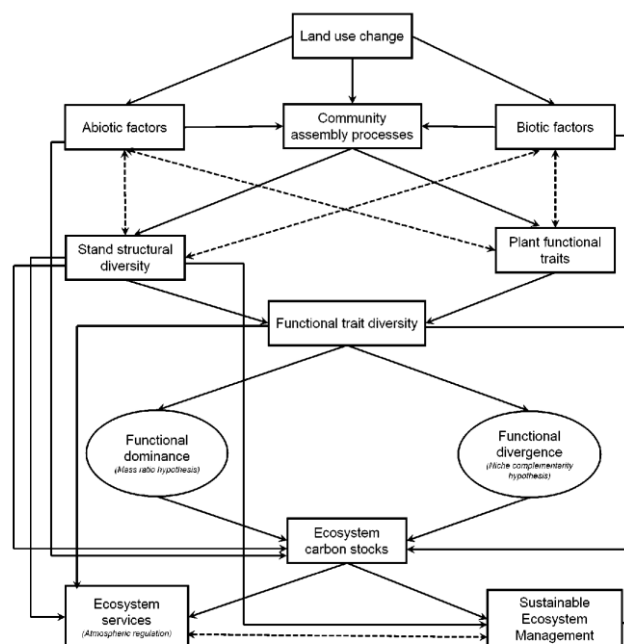


Fig. 3. An integrated conceptual model for the sustainable management of an ecosystem to provides ecosystem services for humans needs. The relationships among environmental factors (abiotic and biotic), community assembly processes, stand structural diversity (species, height and diameter diversity), functional diversity, ecosystem C stocks, ecosystem services and ecosystem management under land use change through anthropogenic activities. Land use change affects the community assembly through environmental filtering, competition and facilitation processes. Plant functional traits and stand structural diversity respond to abiotic and biotic factors on one hand, and affect ecosystem C stocks on the other hand. Functional trait diversity affects ecosystem C stocks through “functional dominance i.e. the mass ratio hypothesis” or/and “functional divergence i.e. the niche complementarity hypothesis”, thus, influences ecosystem services or ecosystem management. The changes in ecosystem C stocks could feed back to abiotic and biotic factors, and ecosystem C stocks may directly affected by stand structural diversity, functional diversity and environmental factors. Stand structural and functional trait diversities may also directly affect the ecosystem services, and hence, provide indications for ecosystem management. Finally, better management of an ecosystem will provide better services for humans needs.

not suitable for calculating the biomass of shrubs and small trees because of the restriction of DBH range (Ali *et al.* 2015). In addition, generalized

allometric equations for various forest ecosystems, such as subtropical forests, are still the subject of debate (Ali *et al.* 2015). However, because of the lack of methodology and difficulty in calculation, the most empirical studies have avoided the shrub vegetation in estimating forest biomass, resulting in an underestimation of the total forest biomass (e.g. Cavanaugh *et al.* 2014; Wang *et al.* 2011). In addition, AGB of forest inventory plots are commonly measured, rather than SOCS. But soil is also a main C pool, which has not been considered in most of the studies reviewed here (Table 1).

Biodiversity measures on the basis of plant functional traits are more important rather than species compositions. A functional group encompasses a set of species with similar morphological, physiological and phenological traits and it can be assumed that species within a functional group provide similar ecosystem services and respond similar to environmental changes (Hooper *et al.* 2005). But most studies reviewed here did not include the potential plant functional traits such as leaf, stem, branch and root traits, for measuring the biodiversity indices while mostly focused on species diversity. Thus, currently, we poorly understood how plant functional and stand structural diversity affect the C stocks in various forest ecosystems. It is very important to consider both mass ratio and niche complementarity hypothesis, when biodiversity–C stocks studies to be explored. Therefore, it is necessary for further research include stand structural diversity (species, size and height), functional diversity (e.g. functional dominance and divergence), and environmental variables (abiotic and biotic factors) to test the mutual and additional contributions of each axis of biodiversity to both ACS and SOCS.

The question is how to manage an ecosystem in a sustainable way to get ecosystem services (e.g., atmospheric regulation) from generation to generation. Functional trait diversity affects atmospheric regulations and ecosystem management through the impact of ecosystem C stocks (Fig. 3). Researchers should fully and accurately understand the relationships between biodiversity and C stocks. Lastly, it is recommended that future studies should include all basic components, not just species diversity or richness, of an ecosystem to fully understand the biodiversity–C stocks relationships for the purpose of managing an ecosystem in a sustainable way (see recommended conceptual model in Fig. 3).

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References

- Aerts, R. & F. S. III. Chapin. 2000. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Advances in Ecological Research* **30**: 1–67.
- Ali, A. 2015. A review of strong evidence for the effect of functional dominance on carbon stocks in natural forest ecosystems. *Research Journal of Forestry* **9**: 65–70.
- Ali, A., M. S. Xu, Y. T. Zhao, Q. Q. Zhang, L. L. Zhou, X. D. Yang & E.R. Yan. 2015. Allometric biomass equations for shrub and small tree species in subtropical China. *Silva Fennica* **49**: 1–10.
- Andelman, S. J. & M. R. Willig. 2003. Present patterns and future prospects for biodiversity in the Western Hemisphere. *Ecology Letters* **6**: 818–824.
- An-Ning, S., J. Tian-Zhen & G. Jiang-Ping. 2008. Relationship between species richness and biomass on environmental gradients in natural forest communities on Mt. Xiaolongshang, northwest China. *Forest Studies in China* **10**: 212–219.
- Baishya, R., S. K. Barik & K. Upadhaya. 2009. Distribution pattern of aboveground biomass in natural and plantation forests of humid tropics in northeast India. *Tropical Ecology* **50**: 295–304.
- Balvanera, P., A. B. Pfisterer, N. Buchmann, J. S. He, T. Nakashizuka, D. Raffaelli & B. Schmid. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters* **9**: 1146–1156.
- Bosworth, D., R. Birdsey, L. Joyce & C. Millar. 2008. Climate change and the nation's forests: Challenges and opportunities. *Journal of Forestry* **106**: 214–221.
- Brown, S., A. J. R. Gillespie & A. E. Lugo. 1989. Biomass estimation methods for tropical forests with

- applications to forest inventory data. *Forest Science* **35**: 881–902.
- Bunker, D. E., F. de-Clerck, J. C. Bradford, R. K. Colwell, I. Perfecto, O. L. Phillips, M. Sankaran & S. Naeem. 2005. Species loss and above-ground carbon storage in a tropical forest. *Science* **310**: 1029–1031.
- Buongiorno, J., S. Dahir, H. C. Lu & C. R. Lin. 1994. Tree size diversity and economic returns in uneven-aged forest stands. *Forest Science* **40**: 83–103.
- Butterfield, B. J. & K. N. Suding. 2013. Single-trait functional indices outperform multi-trait indices in linking environmental gradients and ecosystem services in a complex landscape. *Journal of Ecology* **101**: 9–17.
- Cardinale, B. J., D. S. Srivastava, J. E. Duffy, J. P. Wright, A. L. Downing, M. Sankaran & C. Jouseau. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* **443**: 989–992.
- Cardinale, B. J., J. E. Duffy, A. Gonzalez, D. U. Hooper, C. Perrings, P. Venail, A. Narwani, G. M. Mace, D. Tilman, D. A. Wardle, A. Kinzig, G. C. Daily, M. Loreau, J. B. Grace, A. Larigauderie, D. S. Srivastava & S. Naeem. 2012. Biodiversity loss and its impact on humanity. *Nature* **486**: 59–67.
- Cardinale, B. J., J. P. Wright, M. W. Cadotte, I. T. Carroll, A. Hector, D. S. Srivastava, M. Loreau & J. J. Weis. 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences (USA)* **104**: 18123–18128.
- Cardinale, B. J., K. L. Matulich, D. U. Hooper, J. E. Byrnes, E. Duffy, L. Gamfeldt, P. Balvanera, M. I. O’Conner & A. Gonzalez. 2011. The functional role of producer diversity in ecosystems. *American Journal of Botany* **98**: 572–592.
- Carney, K. M., P. A. Matson & B. J. M. Bohannan. 2004. Diversity and composition of tropical soil nitrifiers across a plant diversity gradient and among land-use types. *Ecology Letters* **7**: 684–694.
- Caspersen, J. P. & S. W. Pacala. 2001. Successional diversity and forest ecosystem function. *Ecological Research* **16**: 895–903.
- Cavanaugh, K. C., J. S. Gosnell, S. L. Davis, J. Ahumada, P. Boundja, D. B. Clark, B. Mugerwa, P. A. Jansen, T. G. O’Brien, F. Rovero, D. Sheil, R. Vasquez & S. Andelman. 2014. Carbon storage in tropical forests correlates with taxonomic diversity and functional dominance on a global scale. *Global Ecology and Biogeography* **23**: 563–573.
- Chalcraft, D. R., B. J. Wilsey, C. Bowles & M. R. Willig. 2009. The relationship between productivity and multiple aspects of biodiversity in six grassland communities. *Biodiversity and Conservation* **18**: 91–104.
- Chave, J., C. Andalo, S. Brown, M. A. Cairns, J. Q. Chambers, D. Eamus, H. Folster, F. Fromard, N. Higuchi, T. Kira, J. P. Lescure, B. W. Nelson, H. Ogawa, H. Puig, B. Riera & T. Yamakura. 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* **145**: 87–99.
- Chen, X. 2006. Tree diversity, carbon storage, and soil nutrient in an old-growth forest at Changbai Mountain, Northeast China. *Communications in Soil Science and Plant Analysis* **37**: 363–375.
- Con, V. T., T. N. Thang, T. D. Thanh-Ha, C. C. Khiem, H. T. Quy, T. V. Lam, V. T. Do & T. Sato. 2013. Relationship between aboveground biomass and measures of structure and species diversity in tropical forests of Vietnam. *Forest Ecology and Management* **310**: 213–218.
- Conti, G. & S. Díaz. 2013. Plant functional diversity and carbon storage – an empirical test in semiarid forest ecosystems. *Journal of Ecology* **101**: 18–28.
- Creed, R. P., R. P. Cherry, J. R. Pflaum & C. J. Wood. 2009. Dominant species can produce a negative relationship between species diversity and ecosystem function. *Oikos* **118**: 723–732.
- De Deyn, G. B., J. H. C. Cornelissen & R. D. Bardgett. 2008. Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecology Letters* **11**: 516–531.
- Díaz, S., J. Fargione, F. S. Chapin & D. Tilman. 2006. Biodiversity loss threatens human well-being. *PLoS Biology* **4**: 1300–1305.
- Díaz, S., J. G. Hodgson, K. Thompson, M. Cabido, J. H. C. Cornelissen, A. Jalili, G. Montserrat-Martí, J. P. Grime, F. Zarrinkamar, Y. Asri, *et al.* 2004. The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science* **15**: 295–304.
- Díaz, S., S. Lavorel, F. de Bello, F. Quétier, K. Grigulis & T. M. Robson. 2007. Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences (USA)* **104**: 20684–20689.
- Dixon, R. K., A. M. Solomon, S. Brown, R. A. Houghton, M. C. Trexler & J. Wisniewski. 1994. Carbon pools and flux of global forest ecosystems. *Science* **263**: 185–190.
- Erskine, P. D., D. Lamb & M. Bristow. 2006. Tree species diversity and ecosystem function: can tropical multi-species plantations generate greater productivity? *Forest Ecology and Management* **233**: 205–210.

- FAO. 2001. *Global Forest Resources Assessment 2000: Main Report*. FAO Forestry Paper 140, FAO, Rome.
- Finegan, B., M. Peña-Claros, A. de Oliveira, N. Ascarrunz, M. S. Bret-Harte, G. Carreño-Rocabado, F. Casanoves, S. Díaz, V. P. Eguiguren, F. Fernandez, *et al.* 2014. Does functional trait diversity predict above-ground biomass and productivity of tropical forests? Testing three alternative hypotheses. *Journal of Ecology* **103**: 191–201.
- Firn, J., P. D. Erskine & D. Lamb. 2007. Woody species diversity influences productivity and soil nutrient availability in tropical plantations. *Oecologia* **154**: 521–533.
- Garnier, E., J. Cortez, G. Billès, M-L. Navas, C. Roumet, M. Debussche, G. Laurent, A. Blanchard, D. Aubry, A. Bellmann, C. Neill & J-P. Toussaint. 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* **85**: 2630–2637.
- Grime, J. P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* **86**: 902–910.
- Hector, A. 1998. The effect of diversity on productivity: detecting the role of species complementarity. *Oikos* **82**: 597–599.
- Hector, A., B. Schmid, C. Beierkuhnlein, M. C. Caldeira, M. Diemer, P. G. Dimitrakopoulos, J. A. Finn, H. Freitas, P. S. Giller, J. Good, *et al.* 1999. Plant diversity and productivity experiments in European grasslands. *Science* **286**: 1123–1127.
- Hooper, D. U. & J. S. Dukes. 2004. Over yielding among plant functional groups in a long-term experiment. *Ecology Letters* **7**: 95–105.
- Hooper, D. U., F. S. III. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, *et al.* 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* **75**: 3–35.
- Houle, G. 2007. Determinants of fine-scale plant species richness in a deciduous forest of northeastern North America. *Journal of Vegetation Science* **18**: 345–354.
- Huston, M. A. 1980. Soil nutrients and tree species richness in Costa Rican forests. *Journal of Biogeography* **7**: 147–157.
- Huy, B. & T. A. Anh. 2008. Estimating CO₂ sequestration in natural broad-leaved evergreen forest in Vietnam. *Asia-Pacific Agroforestry News (FAO)* **32**: 7–10.
- IUCN. 2009. The IUCN red list of threatened species. <http://www.iucnredlist.org/>
- Jonsson, M. & D. A. Wardle. 2009. Structural equation modelling reveals plant-community drivers of carbon storage in boreal forest ecosystems. *Biology Letters* **6**: 116–119.
- Keddy, P. 2005. Putting the plants back into plant ecology: six pragmatic models for understanding and conserving plant diversity. *Annals of Botany* **96**: 177–189.
- Keylock, C. J. 2005. Simpson diversity and the Shannon-Wiener index as special cases of a generalized entropy. *Oikos* **109**: 203–207.
- Kirby, K. R. & C. Potvin. 2007. Variation in carbon storage among tree species: implications for the management of a small-scale carbon sink project. *Forest Ecology and Management* **246**: 208–221.
- Lavorel, S. & K. Grigulis. 2012. How fundamental plant functional trait relationships scale-up to trade-offs and synergies in ecosystem services. *Journal of Ecology* **100**: 128–140.
- Lei, X., W. Wang & C. Peng. 2009. Relationships between stand growth and structural diversity in spruce-dominated forests in New Brunswick, Canada. *Canadian Journal of Forest Research* **39**: 1835–184.
- Lexerød, N. L. & T. Eid. 2006. An evaluation of different diameter diversity indices based on criteria related to forest management planning. *Forest Ecology and Management* **222**: 17–28.
- Liang, J., J. Buongiorno, R. A. Monserud, E. L. Kruger & M. Zhou. 2007. Effects of diversity of tree species and size on forest basal area growth, recruitment, and mortality. *Forest Ecology and Management* **243**: 116–127.
- Lindenmayer, D. & J. Franklin. 1997. Managing stand structure as part of ecologically sustainable forest management in Australian mountain ash forests. *Conservation Biology* **11**: 1053–1068.
- Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B. Schmid, *et al.* 2001. Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science* **294**: 804–808.
- Magurran, A. E. 1988. *Ecological Diversity and its Measurement*. Princeton University Press, Princeton, NJ.
- Magurran, A. E. 2004. *Measuring Biological Diversity*. Blackwell Publishers, Malden, Mass.
- Mason N. W. H., K. MacGillivray, J. B. Steel & J. B. Wilson. 2003. An index of functional diversity. *Journal of Vegetation Science* **14**: 571–578.
- Matthews, E., R. Payne, M. Rohweder & S. Murray. 2000. Forest ecosystem: Carbon Sequestration in Soil. *Global Climate Change Digest* **12**: 19–99.
- McGuire, A. D., S. Sitch, J. S. Clein, R. Dargaville, G. Esser, J. Foley & U. Wittenberg. 2001. Carbon

- balance of the terrestrial biosphere in the twentieth century: analyses of CO₂, climate and land use effects with four process-based ecosystem models. *Global Biogeochemical Cycles* **15**: 183–206.
- Millennium Assessment. 2005. *Ecosystems and Human Well-being: Biodiversity Synthesis*. World Resources Institute, Washington, DC.
- Mittelbach, G. G., C. F. Steiner, S. M. Scheiner, K. L. Gross, H. L. Reynolds, R. B. Waide, M. R. Willig, S. I. Dodson & L. Gough. 2001. What is the observed relationship between species richness and productivity? *Ecology* **82**: 2381–2396.
- Mooney, H., J. Roy & B. Saugier. 2001. *Terrestrial Global Productivity: Past, Present and Future*. Academic Press, San Diego.
- Mouillot, D., W. H. N. Mason, O. Dumay & J. B. Wilson. 2005. Functional regularity: a neglected aspect of functional diversity. *Oecologia* **142**: 353–359.
- Naeem, S., L. Thompson, S. Lawler, J. Lawton & R. Woodfin. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* **368**: 734–737.
- Naeem, S. & Wright, J. P. 2003. Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecology Letters* **6**: 567–579.
- Nakakaawa, C., J. Aune & P. Vedeld. 2009. Changes in carbon stocks and tree diversity in agro-ecosystems in south western Uganda: what role for carbon sequestration payments? *New Forests* **40**: 19–44.
- Negi, J. D. S., R. K. Manhas & P. S. Chauhan. 2003. Carbon allocation in different components of some tree species of India: a new approach for carbon estimation. *Current Science* **85**: 1528–1531.
- Nowak, D. J. & E. J. Greenfield. 2012. Tree and impervious cover change in US cities. *Urban Forestry and Urban Greening* **11**: 21–30.
- Pan, Y., A. R. Birdsey, O. L. Philipps & B. R. Jackson. 2013. The structure, distribution and biomass of the world's forests. *Annual Review of Ecology, Evolution and Systematics* **44**: 593–662.
- Patil, G. P. & C. Taillie. 1979. An overview of diversity. pp. 3-27. In: J. F. Grassle, G. P. Patil, W. K. Smith & C. Taillie (eds) *Ecological Diversity in Theory and Practice*. International Cooperative Publishing House, Fairland, Maryland.
- Phillips, O. L., P. Hall, A. H. Gentry, S. A. Sawyer & R. Vásquez. 1994. Dynamics and species richness of tropical rain forests. *Proceedings of National Academy of Science (USA)* **91**: 2805–2809.
- Poorter, H., Ü. Niinemets, L. Poorter, I. J. Wright & R. Villar. 2009. Causes and consequences of variation in leaf mass per area. (LMA): a meta-analysis. *New Phytologist* **182**: 565–588.
- Pretzsch, H. 1997. Analysis and modeling of spatial stand structures. Methodological considerations based on mixed beech-larch stands in lower Saxony. *Forest Ecology and Management* **97**: 237–253.
- Reich, P. 2011. Taking stock of forest carbon. *Nature Climate Change* **1**: 346–347.
- Ruiz-Jaen, M. C. & C. Potvin 2011. Can we predict carbon stocks in tropical ecosystems from tree diversity? Comparing species and functional diversity in a plantation and a natural forest. *New Phytologist* **189**: 978–987.
- Sagar, R. & J. S. Singh. 2006. Tree density, basal area and species diversity in a disturbed dry tropical forest of northern India: Implications for conservation. *Environment Conservation* **33**: 256–262.
- Sala, O. E., F. S. III. Chapin, J. J. Armesto, E. J. Berlow, R. Bloomfield, E. Dirzo, L. F. Huber-sanwald, R. B. Huenneke, A. Jackson, R. Kinzig, *et al.* 2000. Global biodiversity scenarios for the year 2100. *Science* **287**: 1770–1774.
- Schumacher, J. & C. Roscher. 2009. Differential effects of functional traits on aboveground biomass in semi-natural grasslands. *Oikos* **118**: 1659–1668.
- Shannon, C. E. & W. Weaver. 1949. *The Mathematical Theory of Communication*. University of Illinois Press, Champaign, IL.
- Shannon, C. E. 1948. A mathematical theory of communication. *Bell System Technical Journal* **27**: 379–423.
- Simpson, E. H. 1949. Measurement of diversity. *Nature* **163**: 688.
- Staudhammer, C. L., V. M. LeMay. 2001. Introduction and evaluation of possible indices of stand structural diversity. *Canadian Journal of Forest Research* **31**: 1105–1115.
- Sullivan, T. P., D. S. Sullivan & P. M. F. Lindgren. 2001. Influence of variable retention harvests on forest ecosystems. I. Diversity of stand structure. *Journal of Ecology* **38**: 1221–1233.
- Szwagrzyk, J. & Gazda A. 2007. Above-ground standing biomass and tree species diversity in natural stands of Central Europe. *Journal of Vegetation Science* **18**: 555–562.
- Tilman, D., D. Woding & J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* **379**: 718–720.
- Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie & E. Siemann. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* **277**: 1300–1302.
- Timothy, D., M. Onesimo & I. Riyad. 2016. Quantifying aboveground biomass in African environments: A review of the trade-offs between sensor estimation accuracy and costs. *Tropical Ecology* **57**: 393–405.

- Upadhaya, K., N. Thapa & S. K. Barik. 2015. Tree diversity and biomass of tropical forests under two management regimes in Garo hills of north-eastern India. *Tropical Ecology* **56**: 257–268.
- Vance-Chalcraft, H.D., M. R. Willig, S. B. Cox, A. E. Lugo & F. N. Scatena. 2010. Relationship between aboveground biomass and multiple measures of biodiversity in subtropical forest of Puerto Rico. *Biotropica* **42**: 290–299.
- Varga, P., H. Y. H. Chen & K. Klinka. 2005. Tree-size diversity between single-and mixed-species stands in three forest types in western Canada. *Canadian Journal of Forest Research* **35**: 593–601.
- Vilà, M., J. Vayreda, C. Gracia & J. J. Ibáñez. 2003. Does tree diversity increase wood production in pine forests? *Oecologia* **135**: 299–303.
- Vilà, M., J. Vayreda, L. Comas, J. J. Ibanez, T. Mata & B. Obon. 2007. Species richness and wood production: A positive association in Mediterranean forests. *Ecology Letters* **10**: 241–250.
- Von Felten, S., A. Hector, N. Buchmann, P. A. Niklaus, B. Schmid & M. Scherer-Lorenzen. 2009. Belowground nitrogen partitioning in experimental grassland plant communities of varying species richness. *Ecology* **90**: 1389–1399.
- Waide, R., M. R. Willig, C. F. Steiner, G. Mittelbach, I. Gough, S. I. Dodson, G. P. Juday & R. Parmenter. 1999. The relationship between productivity and species richness. *Annual Review of Ecology, Evolution and Systematics* **30**: 257–300.
- Wang, W., X. Lei, Z. Ma, D. D. Kneeshaw & C. Peng. 2011. Positive relationship between aboveground carbon stocks and structural diversity in spruce dominated forest stands in New Brunswick, Canada. *Forest Science* **57**: 506–515.
- Wardle, D. A., R. D. Bardgett, J. N. Klironomos, H. Setälä, W. H. van der Putten & D. H. Wall. 2004. Ecological linkages between aboveground and belowground biota. *Science* **304**: 1629–1633.
- Wardle, D. A., M. Jonsson, S. Bansal, R. D. Bardgett, M. J. Gundale & D. B. Metcalfe. 2012. Linking vegetation change, carbon sequestration and biodiversity: insights from island ecosystems in a long-term natural experiment. *Journal of Ecology* **100**: 16–30.
- Whittaker, R. J. & E. Heegaard. 2003. What is the observed relationship between species richness and productivity? *Ecology* **82**: 3384–3390.
- Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, T. Chapin, J. H. C. Cornelissen, M. Diemer, *et al.* 2004. The worldwide leaf economics spectrum. *Nature* **428**: 821–827.
- Yu, G., Z. Chen, S. Piao, C. Peng, P. Ciais, Q. Wang, X. Li & X. Zhu. 2014. High carbon dioxide uptake by subtropical forest ecosystems in the East Asian monsoon region. *Proceedings of the National Academy of Sciences (USA)* **111**: 4910–4915.
- Zhang, Y. B., B. L. Duan, J. R. Xian, H. Korpelainen & C. Y. Li. 2011. Links between plant diversity, carbon stocks and environmental factors along a successional gradient in a subalpine coniferous forest in southwest China. *Forest Ecology and Management* **262**: 361–369.

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