Plant functional diversity and carbon storage – an empirical test in semi-arid forest ecosystems

Georgina Conti* and Sandra Díaz

Instituto Multidisciplinario de Biología Vegetal (IMBIV- CONICET) and Departamento de Diversidad Biológica y Ecología, FCEFyN, Universidad Nacional de Córdoba, CC 495, CP 5000 Córdoba, Argentina

Summary

1. Carbon storage in vegetation and soil underpins climate regulation through carbon sequestration. Because plant species differ in their ability to capture, store and release carbon, the collective functional characteristics of plant communities (functional diversity) should be a major driver of carbon accumulation in terrestrial ecosystems.

2. Three major components of plant functional diversity could be put forward as drivers of carbon storage in ecosystems: the most abundant functional trait values, the variety of functional trait values and the abundance of particular species that could have additional effects not incorporated in the first two components.

3. We tested for associations between these components and carbon storage across 16 sites in the Chaco forest of Argentina under the same climate and on highly similar parental material. The sites differed in their plant functional diversity caused by different long-term land-use regimes.

4. We measured six plant functional traits in 27 species and weighted them by the species abundance at each site to calculate the community-weighted mean (CWM) and the functional divergence (FDvar) of each single trait and of multiple traits (FDiv). We also measured plant and soil carbon storage. Using a stepwise multiple regression analysis, we assessed which of the functional diversity components best explained carbon storage.

5. Both CWM and FDvar of plant height and wood-specific gravity, but no leaf traits, were retained as predictors of carbon storage in multiple models. Relationships of FDvar of stem traits and FDiv with carbon storage were all negative. The abundance of five species improved the predictive power of some of the carbon storage models.

6. *Synthesis.* All three major components of plant functional diversity contributed to explain carbon storage. What matters the most to carbon storage in these ecosystems is the relative abundance of plants with tall, and to a lesser extent dense, stems with a narrow range of variation around these values. No consistent link was found between carbon storage and the leaf traits usually associated with plant resource use strategy. The negative association of trait divergence with carbon storage provided no evidence in support to niche complementarity promoting carbon storage in these forest ecosystems.

Key-words: carbon stocks, climate change mitigation, ecosystem services, functional divergence, functional identity, functional traits, land use change, mass ratio hypothesis, niche complementarity, semi-arid Chaco forest

Introduction

Increasingly compelling evidence of global climatic change as a result of rising levels of carbon dioxide in the atmosphere (IPCC 2007) has greatly stimulated the interest in biological carbon (C) sequestration in natural ecosystems, and particularly forests. An effective climate control by terrestrial ecosystems not only depends on the rate of C uptake by primary producers (i.e. their sink capacity), but also on the rate of C release from the biota, the permanence of stocks and the probability of abrupt release due to episodes of natural or human disturbance (Catovsky, Bradford & Hector 2002;

*Correspondence author. Email: gconti@conicet.gov.ar

Schulze, Valentini & Sanz 2002; Díaz, Hector & Wardle 2009a). C stocks at any given point in time reflect the net balance between these uptake, loss and retention processes.

Moreover, because different plant species differ in their ability to capture, store and release C, the collective functional characteristics of plant communities, under a given regional climatic regime, should be a major driver of C sequestration in terrestrial ecosystems (Catovsky, Bradford & Hector 2002; De Deyn, Cornelissen & Bardgett 2008; Thompson *et al.* 2009). One way to conceptualize these functional characteristics of communities is functional diversity, defined as the value, range, distribution and relative abundance of functional traits of the organisms that make up an ecosystem (Díaz *et al.* 2007). This definition of functional diversity includes functional identity and is more comprehensive than those that are explicitly restricted to the variability of traits (e.g. Petchey & Gaston (2006)) and thus is closer to the concept of 'functional structure of communities' proposed by Mouillot *et al.* (2011), also called 'functional composition' by other authors.

A central question here is which plant functional traits should be functionally the most relevant. This is the case as these are the ones that should be measured, in order to characterize functional diversity in situations involving different ecosystem properties of interest. In this respect, there is now an important body of literature pointing to the plant functional traits and trait syndromes that should be most important, specifically for C storage at the ecosystem level. The amount of wood in the vegetation and its C content clearly drive the total amount of C stored above-ground and below-ground. Plants traits associated with a larger biomass and a higher investment in structure per unit of biomass, such as height and wood-specific gravity (WSG), are therefore expected to directly influence above-ground and below-ground ecosystem C storage (Baker *et al.* 2004; Moles *et al.* 2009). Larger plants are also expected to shed more biomass in the form of leaf and woody litter per unit ground area and thus contribute directly to C accumulation in the standing litter and in the organic soil (Garnier *et al.* 2004; Lavorel & Grigulis 2012). Functional traits related with plant tissue quality, such as WSG, leaf nutrient concentration, leaf area displayed per unit C and leaf toughness (LT), also influence the residence time of both living tissues and litter and therefore indirectly influence C storage in the soil (Aerts & Chapin 2000; Chapin 2003; Wardle *et al.* 2004; De Deyn, Cornelissen & Bardgett 2008). In particular, there is evidence of a trade-off between a suite of attributes promoting fast C acquisition and fast decomposition and another suite of attributes which promote the conservation of resources within well-protected tissues and slow decomposition (Grime 1979; Grime *et al.* 1997; Reich, Walters & Ellsworth 1997; Díaz *et al.* 2004; Wright *et al.* 2004). This trade-off, called the acquisition vs. 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. For example, acquisitive resource use syndromes are characterized by the combination of attributes such as high specific leaf area (SLA), high leaf concentration

of nitrogen (LNC) and phosphorous, low LT and low leaf dry matter content (LDMC), which are consistently associated with high C input through photosynthesis and also high C losses through decomposition (e.g. Herms & Mattson 1992; Grime *et al.* 1996, 1997; Díaz *et al.* 2004; Wright *et al.* 2004; Poorter & Garnier 2007; Cornwell *et al.* 2008; Poorter *et al.* 2009; Freschet, Aerts & Cornelissen 2012). Conservative syndromes are characterized by the opposite attributes. 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 (Wardle *et al.* 2004; De Deyn, Cornelissen & Bardgett 2008; Díaz, Hector & Wardle 2009a).

Another crucial aspect in the investigation of the links between functional diversity and ecosystem properties is that major components of functional diversity, most prominently the trait values of the most abundant species (sometimes called 'functional identity') or the variety of trait values present in the community (called 'functional diversity' by other authors), are the most strongly associated with ecosystem functionality. These components have often been associated with different mechanistic models of diversity effects on ecosystem properties. According to the mass ratio hypothesis, proposed by Grime (1998), the role of species in the ecosystem is proportional to their biomass; therefore, the most abundant values of plant functional traits will be the main determining factors of the total C stored in the ecosystem above- and below-ground compartments (Díaz, Hector & Wardle 2009a). On the other hand, according to the niche-complementarity hypothesis (Trenbath 1974), the coexistence of different functional strategies, embodied in the presence of diverging values of functional traits, such as stratified mixtures of sun-adapted species in the overstorey and shade-adapted species in the understorey (Pretzsch 2005; Lavorel & Grigulis 2012), or the combination of species with different rooting patterns (Davis & Mooney 1986; Sala *et al.* 1989) should lead to a fuller resource exploitation by the plant community as a whole across time and space. This should be reflected in higher standing biomass, which could directly lead to enhanced C storage in plant biomass and also in soil through higher input of senescent material (Scherer-Lorenzen, Bonilla & Potvin 2007). The presence of senescent material of contrasting quality (i.e. different LT or nutrient concentration) has also been reported to affect litter decomposition rate and thus soil C storage. However, it cannot be strictly considered as part of the niche-complementarity effect, and the direction of these effects varies widely and seems to be strongly context-dependent (Hättenschwiler, Tiunov & Scheu 2005; Nadrowski, Wirth & Scherer-Lorenzen 2010).

The mass ratio and niche-complementarity models are not necessarily mutually exclusive; both have been shown to operate in natural ecosystems and can have different relative importance in different situations (Potvin & Gotelli 2008; Díaz, Hector & Wardle 2009b; Mouillot *et al.* 2011). In addition, idiosyncratic effects of particular species are common (Scherer-Lorenzen, Bonilla & Potvin 2007; Díaz, Hector & Wardle 2009b). Consequently, Díaz *et al.* (2007) proposed a

conceptual and analytical approach to test them simultaneously 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 costly.

Most of the evidence of the effect of functional plant composition on ecosystem processes has been derived from experiments on highly simplified systems (Tilman *et al.* 1997; Thompson *et al.* 2005; Fornara & Tilman 2008; Steinbeiss *et al.* 2008; De Deyn *et al.* 2009; Pakeman, Eastwood & Scobie 2011; Roscher *et al.* 2012). Whilst this has the advantages of experimental design and control of covarying factors, it has the disadvantage of not necessarily representing the most important mechanisms operating in real ecosystems (Leuschner, Jungkunst & Fleck 2009). Some authors have experimentally removed species or functional groups from initially homogeneous communities in the field, both herbaceous (Symstad & Tilman 2001; Polley *et al.* 2006; McLaren & Turkington 2010; Joner *et al.* 2011) and woody (Aguiar & Sala 1994; Díaz *et al.* 2003; Bret-Harte *et al.* 2008; Wardle, Lagerström & Nilsson 2008; Urcelay *et al.* 2009). However, in forest communities, experimental manipulation is prohibitively costly. Several studies have taken advantage of mixed-species and mono-specific tree plantations (e.g.Vilà *et al.* 2003; Pretzsch 2005; Erskine, Lamb & Bristow 2006; Firn, Erskine & Lamb 2007; Scherer-Lorenzen, Bonilla & Potvin 2007; Scherer-Lorenzen *et al.* 2007; Vilà *et al.* 2007; Nadrowski, Wirth & Scherer-Lorenzen 2010; Potvin *et al.* 2011), but these experiments do not necessarily mimic the species richness, age structure and combination of growth forms typical of naturally established forests. Just a few studies have compared the effect of different levels of functional diversity in natural forest or evaluated the importance of specific functional traits for different ecosystem processes within natural forest ecosystems (Caspersen & Pacala 2001; Mayfield *et al.* 2005; Delagrange *et al.* 2008; Jonsson & Wardle 2010; Ruiz-Jaen & Potvin 2011; Wardle *et al.* 2012). In summary, empirical studies of the links between functional trait composition and C storage in naturally established forest ecosystems are still very rare.

In this paper, we aimed to investigate the effects of plant functional diversity on C storage in ecosystems of the semi-arid Chaco forest of Córdoba, Argentina. Using the approach of Díaz *et al.* (2007), we tested for associations between different components of functional diversity (most abundant functional trait values, variety of functional trait values and the abundance of particular species) and C storage in different ecosystem compartments. Specifically, we tested the hypotheses that, under the same climatic and soil parent material conditions:

1 Functional diversity affects C storage in the standing vegetation, litter and soil via the effects of the dominant (locally most abundant) functional trait values on C dynamics. Plant communities dominated by plants with a higher investment in structure (taller and with a denser stem) and showing a more conservative resource use syndrome (lower values of SLA and LNC, higher values of LDMC and LT) should accumulate more C in standing biomass; this should also lead to a larger C stock in the soil, because of a higher C input and a longer C residence time.

2 Functional diversity affects C accumulation in plant and soil stocks via the effects of the presence of diverging functional trait values on C dynamics. The coexistence of plants with contrasting functional trait values should lead to a fuller use of resources by the community as a whole and thus to higher biomass production and higher C input into the soil, increasing both above-ground and soil C stocks.

Materials and methods

STUDY AND EXPERIMENTAL DESIGN

The study was carried out in the southern extreme of the Gran Chaco, in central Argentina (*c.* 31°17′–31°50′ S and 65°16′–65° 32′ W). The climate is subtropical with a mean annual precipitation of 600 mm distributed in spring–summer (October–March) and a mean annual temperature of 18 °C. Soils are mainly sandy-loam aridisols of alluvial origin (Gorgas & Tassile 2003). The dominant vegetation is a xerophytic forest with the trees *Aspidosperma quebracho-blanco* and *Prosopis flexuosa* as canopy and subcanopy dominants, respectively. The shrub layer is often dense and dominated by *Mimozyganthus carinatus*, *Acacia gilliesii* and *Larrea divaricata* (Cabido *et al.* 1992). At present, the Chaco primary forest can only be found in very small patches embedded in a mosaic of other types of vegetation in different stages of succession or deterioration, as a result of land use, including logging, livestock grazing and cultivation of annual crops, with different degrees of intensification (Zak, Cabido & Hodgson 2004). Previous studies suggest that these different ecosystems store different amounts of C and that such differences cannot be attributed to differences in climate or soil parental material (Bonino 2006).

Our research questions required enough variation in plant functional diversity whilst keeping abiotic factors as constant as it is possible in the field. To this end, within the study area, we selected 16 sites corresponding to different ecosystem types, characterized by the presence of plant communities with different taxonomic and functional diversity: primary forest, secondary forest, closed species-rich shrubland and open shrubland strongly dominated by *L. divaricata*. These different ecosystem types initially corresponded to the same vegetation, developed under the same climate and on highly similar parental material, and were derived from it by different long-term land-use regimes. These consisted of combinations of different intensities of extensive livestock grazing and logging (Cabido *et al.* 1994). There were no records or physical signs of fire, ploughing or application of soil fertilizer in any of the plots during the past few decades, and on the basis of historical sources, they were unlikely to have been tilled during at least the past 150 years. Sites were located at a distance of at least 1 km apart. At each site, we established a homogeneous 50 × 50 m plot (replicate) to carry out vegetation and soil sampling. Although initially the sites were chosen to match these four different categories, they actually represent a continuum rather than discrete categories, because of the nature of the land-use regimes. Accordingly, there were marked overall similarities in the general properties of the soils. A description of the land-use regime, soil and vegetation characteristics of the different ecosystem types is provided in Table S1 (see Supporting Information).

CARBON STORAGE

In each 50×50 m plot, we quantified C in woody and herbaceous standing vegetation, litter and soil organic C (SOC) to a depth of 30 cm. All C stocks were expressed in Mg C ha^{-1} (Table S2).

We surveyed all trees > 5 cm diameter at breast height (d.b.h.) in each of the 50×50 m plots and estimated their dry biomass using the allometric model proposed by Brown (1997) for dry forests. A total of 969 trees were measured across all plots. Although more recent allometric models exist (e.g. Chave *et al.* 2005), we chose this equation because it does not include height (H) or WSG, which are functional traits included in the analysis of functional diversity; this avoids any circularity in linking C storage with functional diversity. The allometric model proposed by Brown (1997) used in this study to estimate individual tree above-ground dry biomass (AGB*t*) had the following form:

$$AGBt = \exp(-0.535 + \log_{10}(BA)), \qquad \text{eqn 1}$$

where BA corresponded with basal area (cm^2), calculated as $\pi*(\text{d.b.h.}/2)^2$, where d.b.h. corresponded to diameter at the breast height (cm).

This equation tended to underestimate individual tree biomass as compared to the estimations obtained using Chave *et al.*'s (2005) model for dry forests, but the results of the two models were highly consistent ($R^2 = 0.95$, $P < 0.0001$; see Fig. S1).

For shrub biomass estimation, we established three 5×5 m subplots randomly distributed within each 50×50 m plot. In each subplot, we sampled all shrubs (i.e. multi-stemmed individuals) and small trees (< 5 cm d.b.h.). A total of 772 individuals were measured across all plots. We estimated individual shrub above-ground dry biomass (AGB*s*) using a general multi-species equation developed locally ($n = 245$, $R^2 = 0.76$, $P < 0.0001$). This equation was crown-based and therefore did not include any of the traits used to estimate functional diversity. The form of the equation is presented below; more details on its development and its advantages with respect to non-crown-based equations are presented elsewhere (G. Conti *et al.*, unpub. data):

$$ABGs = 1.176 \times \exp(-9.58 + 0.86(\text{Ln}(CA)) \qquad \text{eqn 2}$$

where CA = crown area (cm^2)

We converted plant woody biomass to C multiplying it by a factor of 0.5, since C roughly represents 50% of dry woody biomass (Brown 1997).

We quantified dry biomass of herbaceous vegetation by harvesting all above-ground herbaceous biomass in six subplots (0.5×0.5 m) randomly distributed within each 50×50 m plot during the peak of the growing season (summer). The amount of litter was quantified by measuring the accumulated fine woody debris and leaf litter in autumn, after most of the senescent parts of deciduous and semi-deciduous species material had fallen. This was done by a single collection of all plant material accumulated on the ground surface in six subplots (0.5×0.5 m) randomly distributed within each plot. A subsample of litter and herbaceous vegetation collected at each subplot was oven-dried at 80 ° C for 3 days, weighed, ground and kept in a muffle furnace (INDEF mod. 331) at 500 °C for 4 h to obtain the ash content of the subsample (Schlesinger & Hasey 1981), following a loss-in-ignition approach. Organic C content was taken as 50% of ash-free dry mass (Schlesinger 1977). This value was used as a factor to convert total dry biomass in each subplot to C. Standing dead trees and coarse woody debris > 5 cm diameter were initially sampled, but they were not included in the final calculations because their distribution in the field has extremely heterogeneous, and at least in some cases, it is likely to be associated with human redistribution activities. Because overall this compartment represented only

c. 3% of the total C accumulated, their exclusion is unlikely to affect our results.

The sum of woody (AGB*t* and AGB*s*) and herbaceous vegetation represented the above-ground standing biomass C compartment (AGB, Mg C ha^{-1}). Fine woody debris and leaf litter represented the above-ground litter C compartment (AL, Mg C ha^{-1}).

The SOC stock was quantified by collecting soil from the top 30 cm. We collected three samples per plot using a soil corer of 10 cm in diameter and combined them to obtain a composite sample. Samples were air-dried, sieved through a 2-mm mesh and analysed for organic C (g kg^{-1}) using an oxidation in acid medium procedure ('Walkley & Black', Nelson & Sommers 1996). This method was selected to avoid any bias in the estimation due to the presence of carbonates below 10 cm depth (Mazzarino *et al.* 1991), a common feature of soils found in arid and semi-arid environments (Lal 2004). We calculated soil bulk density by measuring the mass of dry soil contained in a metal cylinder which measured 4.5 cm in diameter and 10 cm in height. The samples were oven-dried at 105 °C for 24 h to obtain the dry mass of the soil (Maynard & Curran 2008). No adjustment for rocks or coarse fragments was necessary because the soil samples did not contain any. SOC (Mg C ha^{-1}) in the 0–30 cm layer was quantified by multiplying organic C content (g kg^{-1}), depth (cm) and soil bulk density (g cm^{-3}). The use of a higher number of soil subsamples per plot was not possible due to logistic constraints. However, the results obtained were within the range of those reported by Bonino (2006) for the first 20 cm of soil in the same study area and ecosystem types, on the basis of a considerably larger sampling effort.

Finally, we calculated total ecosystem C (TEC) by adding AGB, AL and SOC.

FUNCTIONAL DIVERSITY

To estimate the relative abundance of different species and trait values in the different plant communities, we carried out a floristic survey of each 50×50 m plot at the peak of the growing season, recording the identity and percentage cover (at 5% intervals) of all plant vascular species present in the plot, according to the methodology of Cabido *et al.* (1993) and Díaz, Cabido & Casanoves (1998). Dominant species were selected as those that together constituted at least 75% of the total community coverage, including woody and herbaceous vegetation (Cornelissen *et al.* 2003; Pakeman & Quested 2007; Lavorel *et al.* 2008). Although in the case of tree species we could have made BA calculations on the basis of d.b.h. obtained for each individual tree, we chose to use cover because (i) it allowed the calculation of functional diversity for the whole vegetation, including the herbaceous component, and (ii) it avoided potential circularity derived from using d.b.h. in the calculation of both functional diversity and C storage. Species abundance thus corresponds to the relative cover of each species relative to the total plant cover in the plot, expressed as a percentage. The species included in the study and their average covers across the study area are shown in Table S3.

We selected six key functional traits that are known or expected to affect ecosystem processes associated with C dynamics and storage. These were LDMC (mg g^{-1}), LNC (mg g^{-1}), LT measured as tensile strength (N mm^{-1}), leaf area displayed per unit of C, measured as SLA (mm^2 mg^{-1}), plant height (H, cm) and WSG (g cm^{-3}), measured as the ratio of the oven-dried mass of a wood sample divided by the mass of water displaced by its green volume, following Chave *et al.* (2005).

Functional traits of all dominant species reported in this article were measured in the field following standard methodologies, on at least six different healthy, sexually mature individuals (replicates) per species (Cornelissen *et al.* 2003), or obtained from a plant trait database of central-western Argentina (CORDOBASE, included in the TRY global database, Kattge *et al.* 2011). The functional trait values for all the species included in the study are presented in Table S3.

MEASUREMENT OF FUNCTIONAL DIVERSITY COMPONENTS

To test the strength of the association of different functional diversity components with C storage, we used the approach of Díaz *et al.* (2007). This framework distinguishes three different generic components of functional diversity, the dominant (locally most abundant) trait values, the variety (divergence) of trait values and the abundance of particular species.

Dominant trait values in each plot were expressed as the community-weighted mean (CWM), calculated as the averaged trait value in the community, weighted by the species abundance (Garnier *et al.* 2004):

$$\text{CWM}(\text{trait}_X) = \sum p_i x_i, \qquad \text{eqn 3}$$

where *CWM* (trait$_X$) is the CWM for a *X* trait, p_i is the relative cover of species *i* in the community and x_i is the trait value for the species *i*. This metric represents the expected functional trait value of a random community sample (Díaz *et al.* 2007).

Variety of individual trait values was expressed by the functional trait divergence index (FDvar; Mason *et al.* (2003)), which basically represents the variance in trait values, weighted by the abundance of each species in the community, and is calculated as follows:

$$\text{FDvar} = 2/\pi \arctan(5V) \ \text{ and } \ V = \sum p_i (\ln x_i - \ln x)^2 \qquad \text{eqn 4}$$

where x_i is the trait value for the species *i* and $p_i = a_i/\Sigma a_i$, where a_i is the relative cover of the species *i* in the community (Pla, Casanoves & Di Rienzo 2012). FDvar values range between 0 and 1. We selected FDvar over other functional dissimilarity indices due to its relatively simple calculation and interpretation, because it incorporates relative abundance and because it has demonstrated good performance (Mokany, Ash & Roxburgh 2008; Pakeman, Lennon & Brooker 2011).

We calculated functional divergence across multiple traits using the multifunctional index FDiv, which quantifies how species diverge in their distances (weighted by their abundance) from the centre of gravity in the multi-trait functional space (Villéger, Mason & Mouillot 2008). We chose this metric because it is a close multi-trait analogue of FDvar and has also been successfully applied to empirical studies with general objectives similar to ours (e.g. Mouillot *et al.* 2011; Pakeman 2011; Navas & Fayolle 2012). FDiv should be closely related to complementarity effects and is largest when functionally different species, *that is,* with large trait differences, reach similar high abundances (Mouchet *et al.* 2010). As FDvar, it can take values between 0 and 1.

All functional metrics were calculated using the statistical package FDiversity v. 2011 (Casanoves *et al.* 2010). A summary of the variables used in the quantification of functional diversity and C storage is shown in Table S2.

ASSOCIATIONS BETWEEN FUNCTIONAL DIVERSITY AND ECOSYSTEM PROCESSES

To test for links between C storage and the different components of functional diversity, we followed the sequential procedure proposed by Díaz *et al.* (2007). We first used simple linear regression analysis to test for pairwise associations between C storage in different ecosystem compartments and components of functional diversity. All the variables that significantly explained C storage in the pairwise analyses were then included in multiple linear regressions analysis, following a stepwise model selection procedure (Burnham & Anderson 2002), to select the best predictors of C storage in different ecosystem compartments. Statistical analyses were carried out using the statistical package Infostat v. 2011p (Di Rienzo *et al.* 2011).

To test for the idiosyncratic effects of particular species, the abundance (% cover) of each species was included as an additional variable in the final model. A particular species was assumed to have an idiosyncratic effect on C storage (i.e. an effect not included in its contribution to CWM or divergence) if the inclusion of its abundance significantly improved the predictive power of the model after significant CWM and divergence effects had been incorporated ($P < 0.05$, SS type I). For species which have a significant effect on final model, the significance (*P*) of the variable in the model was reported.

To avoid any possible effects of land use on C storage not mediated by CWM or divergence, we evaluated the significance of including ecosystem type as an additional variable in the final models ($P < 0.05$).

Results

A number of individual components of functional diversity were significantly associated with C storage in different ecosystem compartments (Table S4 and Fig. 1). Among leaf traits, none of the CWMs (LDMC, LNC, LT or SLA) explained the variations in C storage in the ecosystem compartments analysed. The FDvar of LNC significantly and positively predicted C storage in all compartments except in the above-ground standing biomass. The FDvar of LT significantly and positively explained C storage in both the soil and the total C ecosystem compartments, but not in the plant ones. Neither the FDvar of LDMC nor that of SLA was significantly associated with C storage. Among stem traits, the CWMs of H and WSG significantly and positively predicted C storage in all compartments, with the exception of the link between WSG and the SOC compartment, which was not significant. The FDvar of the same traits significantly and negatively predicted C storage in all compartments, except for the FDvar of H not being significantly associated with the above-ground standing biomass and soil C stocks. The multi-trait divergence index (FDiv) significantly and negatively predicted C storage in all ecosystems compartments, but its association with the C stored in the above-ground standing biomass was not significant.

Because the possibility existed that no individual leaf trait but combinations of leaf traits (i.e. functional syndromes) would explain C storage, we ran a multivariate analysis (PCA) of the sites on the basis of their trait CWMs. The results (Table S5) confirmed our findings for individual traits. The first multivariate axis (PC 1) was mostly defined by leaf traits and spanned between predominantly 'conservative' and 'acquisitive' extremes. We thus tested the association between the site scores along PC 1 (used as indicators of the predominant resource-use syndrome in their vegetation) and their C storage in different compartments. We found no significant
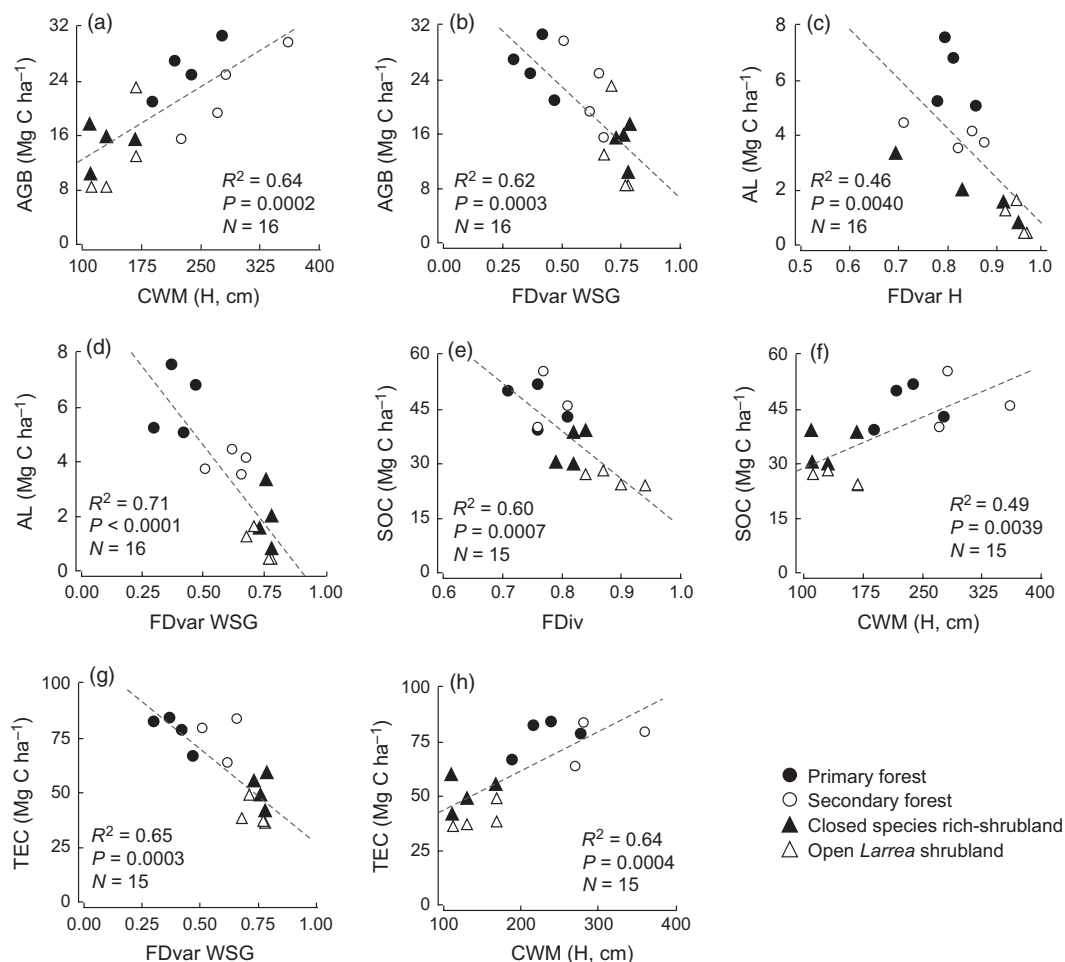
Fig. 1. Simple linear regression analyses between the magnitude of C stocks and functional diversity components in different ecosystems of the semi-arid Chaco of central Argentina. Only variables included in the multiple linear regression analysis (see Table 1) are shown. (a) Above-ground standing biomass carbon (AGB) as a function of the community-weighted mean of height (CWM H); (b) AGB as a function of the functional divergence of wood-specific gravity (FDvar WSG); (c) above-ground litter carbon (AL) as a function of the functional divergence of height (FDvar H); (d) AL as a function of the FDvar WSG; (e) soil organic carbon (SOC) as a function of the multi-trait functional divergence (FDiv); (f) SOC as a function of the CWM of height (CWM H); (g) total ecosystem carbon (TEC) as a function of the FDvar WSG; (h) TEC as a function of the CWM of height (CWM H).*$P < 0.05$; **$P < 0.01$, ***$P < 0.001$.

relationship. The second multivariate axis (PC 2) was defined by H and WSG. The scores of the sites along this axis, not unexpectedly, were significantly and positively associated with C storage in all ecosystem compartments. These results indicated that in this particular study no significantly new insight could be obtained using functional trait syndromes (expressed by scores along multivariate axes); therefore, we only used individual traits in the multiple linear regression models.

When all those functional diversity components that significantly predicted C storage in one or more ecosystem compartments were combined in multiple linear regression models, only the single-trait indices associated with stem traits and the multi-trait index were retained in the final models (Table 1). C storage in the above-ground standing biomass was best predicted negatively by the FDvar of WSG and positively by the CWM of H. C storage in the above-ground litter was best predicted negatively by the FDvar of WSG and H. SOC was

best predicted negatively by the multi-trait divergence index and positively by the CWM of H. Finally, TEC was best predicted negatively by the divergence of WSG (negatively) and the CWM of H (positively).

The incorporation of individual species abundance as an additional variable significantly improved the predictive power of the models of all C compartments with the exception of the above-ground standing biomass. Only one species, the shrub *Moya spinosa*, significantly improved the prediction of C storage in the above-ground litter ($P = 0.0168$), whereas the woody species *Celtis erhenbergiana* ($P = 0.0307$) and *Geoffroea decorticans* ($P = 0.0222$), and the grasses *Trichloris crinita* ($P = 0.0068$) and *Gouinia paraguayensis* were found to improve the prediction of SOC. Same species, excepting *C. erhenbergiana*, appeared as significant predictor variables in the TEC final model (*T. crinita*, $P = 0.0055$; *G. paraguayensis*, $P = 0.0347$ and *Geoffroea decorticans*, $P = 0.0431$). We therefore included them in an alternative

Table 1. Final models obtained from multiple linear regression analysis between the magnitude of C stocks and functional diversity components in different ecosystems of the semi-arid Chaco of central Argentina, using a stepwise ascending procedure. All multiple regression models were statistically significant ($P < 0.05$). R^2, regression adjusted coefficient for the multiple regression model; N, number of sites in the analyses; slope and P refer to individual predictor variables in the final model; CWM H, community-weighted mean of height; CWM WSG, CWM of wood-specific gravity; FDvar WSG, functional divergence of wood-specific gravity; FDvar H, functional divergence of height; FDiv, multi-trait functional dissimilarity index. The ecosystem type effect was added in all multiple regression models, but was non-significant ($P > 0.05$) in all cases

Response variable	Model form	Predictor variables	Slope	P	N	R^2
Above-ground standing biomass carbon (AGB)	AGB = 22.52 − 21.03 FDvar WSG + 0.05 CWM H	*Model*		0.0001	16	0.73
		FDvar WSG	−	0.0184		
		CWM H	+	0.0121		
Above-ground litter carbon (AL)	AL = 18.6 − 9.51 FDvar WSG − 11 FDvar H	*Model*		< 0.0001	16	0.83
		FDvar WSG	−	< 0.0001		
		FDvar H	−	0.0037		
	AL = 14.30 − 6.22 FDvar WSG − 9.17 FDvar H + 0.38 *Moya spinosa*	*Model*		< 0.0001	16	0.89
Soil organic carbon (SOC)	SOC = 108.85 − 102.21 FDiv + 0.06 CWM H	*Model*		0.0001	15*	0.74
		FDiv	−	0.0018		
		CWM H	+	0.0089		
	SOC = 104.24 − 101.49 FDiv + 0.07 CWM H + 0.72 *Trichloris crinita*	*Model*		< 0.0001	15*	0.86
	SOC = 104.69 − 95.70 FDiv + 0.05 CWM H + 1.79 *Geoffroea decorticans*	*Model*		< 0.0001	15*	0.83
	SOC = 108.19 − 105.14 FDiv + 0.07 CWM H + 1.06 *Gouinia paraguayensis*	*Model*		< 0.0001	15*	0.83
	SOC = 112.48 − 102.33 FDiv + 0.03 CWM H + 0.77 *Celtis erhenbergiana*	*Model*		0.0001	15*	0.82
Total ecosystem carbon (TEC)	TEC = 72.73 + 0.11 CWM H − 55.58 FDvar WSG	*Model*		0.0001	15*	0.75
		FDvar WSG	−	0.0151		
		CWM H	+	0.0202		
	TEC = 72.61 + 0.12 CWM H − 63.51 FDvar WSG + 1.30 *T. crinita*	*Model*		0.0001	15*	0.87
	TEC = 71.18 + 0.12 CWM H − 59.94 FDvar WSG + 1.81 *G. paraguayensis*	*Model*		0.0001	15*	0.82
	TEC = 80.58 + 0.08 CWM H − 61.56 FDvar WSG + 2.89 *Geoffroea decorticans*	*Model*		0.0001	15*	0.81

*Soil sample for one site was lost during the laboratory procedure.

predictive model of the C stored in the above-ground litter, soil and the total ecosystem stocks.

Discussion

This study is one of the first to empirically and explicitly test the links between different components of functional diversity and C storage in woody ecosystems in the field, using sites with different plant trait community composition as a consequence of different historical and present management regimes. Although our study did not involve manipulative experiments and therefore causation cannot strictly be claimed, our results show clear trends that can be discussed in the light of current theory.

Our final models showed that all major components of functional diversity – dominant trait values, the variety of trait values present in the community and the presence of particular species – contributed to explain C storage in semi-arid Chaco ecosystems. Our findings also illustrate (in accordance with Fukami & Wardle 2005; Vilà *et al.* 2005) the potential of the study of spatial variation in functional structure driven by anthropogenic use for the assessment of the C sequestra-

tion of real landscapes, particularly when other intervening factors, such as climate, topography and soil parent material, can be controlled.

We found that among the dominant trait values only H was included in final models as the best predictor of C stored in the above-ground standing biomass and in the TEC stock, with a positive relationship. This means that plots where land management had led to the local dominance of shorter-statured plants were associated with lesser C storage in vegetation and soil. This is similar to the results reported by Ruiz-Jaen & Potvin (2011) for natural tropical forests in Panama, and it is not surprising considering that height is a good predictor of total biomass of the plants (Chave *et al.* 2005), which directly influences the amount of C contained in both the above- and below-ground portions of the standing vegetation and incorporated into the soil as litter at senescence (De Deyn, Cornelissen & Bardgett 2008; Lavorel & Grigulis 2012).

WSG was also expected to have a positive effect on C storage, on the basis of both theory (Chave *et al.* 2009; Moles *et al.* 2009; Falster *et al.* 2011) and previous empirical studies (Baker *et al.* 2004; Chave *et al.* 2005), and appeared to have

a significant positive effect according to the individual regression analyses. However, it was not retained as a predictor in the final model. Having shown in the multivariate analysis (Table S5) that height and WSG were on the same axis (PC 2), the significant effects of WSD in single models could simply drop out of the multiple models due to correlation with H (R^2 = 0.66, P = 0.01). Additionally, it also could suggest that the abundance of larger plants, which in this case are not the ones with the densest wood (see Table S3), could be more important than the WSG of the standing and decomposing material in explaining C storage in these ecosystems.

Although leaf traits are known to be involved in the conservation–acquisition trade-off and thus expected to be significant drivers of C dynamics, we did not find a significant relationship between any of the individual leaf traits analysed – or their combination – and plant or soil C storage. Therefore, in the case of plant height, our findings supported our hypothesis (i) that the dominant plant traits – H and to a much lesser degree WSG – predict ecosystem C storage, in accordance with the mass ratio model. However, we found no evidence in support of our expectation that C storage increases with the dominance of leaf trait values, which is symptomatic of a conservative resource use syndrome. This discrepancy with expectations could be due to the fact that we deliberately chose to keep all sources of variation other than plant community composition as constant as possible. As a result, all plots analysed shared very similar climatic and soil parental material conditions, leading to relatively small differences in terms of functional syndromes (Wardle *et al.* 2004; De Deyn, Cornelissen & Bardgett 2008). The fact that there was no sharp species turnover (i.e. ecosystem types were relatively similar in terms of the identity of the dominant species) despite strong differences in the relative abundances of such species points in the same direction. Above-ground disturbance of the kind that produced functional trait composition differences among these plots (i.e. logging, livestock grazing) tends to alter relative abundances rather than the functional identity of communities, especially in areas with relatively long disturbance history (Bond & Midgley 2003; Cingolani, Noy-Meir & Díaz 2005).

The variety of stem trait values, expressed as the FDvar of WSG and H, best explained C storage in above-ground standing biomass, litter and TEC ompartments, but the relationship was negative in all cases (Table 1 and Fig. 1). This was mainly because the WSG or H value distribution in plots with low divergence of WSG or H was concentrated towards high values. In other words, plots with more homogenous WSG or H were dominated by denser-wooded or taller plants, respectively. Plots with higher FDvar had a more even distribution of H or WSG and therefore lower CWMs of H or WSG. This means that the effect of stem traits divergence on C storage ultimately depended on their associated CWM.

The variety of leaf trait values, in particular that of LNC and LT, was positively associated with C storage in the individual regressions analysis. More than a direct effect of the variety of leaf quality on C stocks, this could be related to the fact that plots dominated by large trees that produce large amounts of litter (the major driver of C accumulation according to our findings) had a rich understorey with species with highly contrasting leaf qualities. For example, both *Justicia squarrosa* and *Bromelia urbaniana* are typical members of the community in plots dominated by large trees. The leaves of the former are about three times richer in N and ten times less tough than those of the latter (Table S3), which contributes to increase the divergence of LNC and LT values, despite the fact that these two species represent only a very small contribution to either standing biomass (Table S3) or litter (N. Pérez-Harguindeguy, pers. comm.). In any case, none of the FDvar indices for leaf traits was retained in the final models. Multi-trait divergence, as expressed by FDiv, was negatively associated with C storage. Therefore, we found no evidence to support hypothesis (ii) which, on the basis of the niche-complementarity model, stated that a higher functional trait divergence in the plant community should be associated with larger C storage in the ecosystem.

The fact that the final models predicting C storage in most of the ecosystem compartments were significantly improved by incorporating the abundance of particular species would in principle suggest that species-driven idiosyncratic effects are important, as suggested by several previous studies (e.g. Firn, Erskine & Lamb 2007; Vilà *et al.* 2007; Delagrange *et al.* 2008; Potvin *et al.* 2011).

However, it is not clear whether the abundance of such species is likely to be a causal driver of C storage, or simply a response variable to the presence of particular functional community structures. For example, *M. spinosa* is a significant predictor of C in the above-ground litter compartment, however, considering its low abundance, relatively small size and evergreen to semi-deciduous habit (Table S3), this species is unlikely to be a major driver of litter amount or composition. The only species which appear abundant enough and shed enough litter (or standing dead leaf material that gets slowly incorporated into the soil) to have a potential effect on C dynamics are the shrub *C. erhenbergiana* and the perennial grass *T. crinita*. In conclusion, it is not clear whether any of these species whose abundance helps predicting C storage in some ecosystem compartments are causal factor in the C accumulation process or – perhaps more likely in some cases – only indicators of particular functional community structures (e.g. canopies dominated by large trees) that in turn favour C accumulation. The experimental assessment of their role, although feasible (e.g. using removal experiments), has to be carried out on a case-by-case basis. In the meantime, the abundance of these species can be used to improve the predictive power of the models of C storage, especially considering that they are regionally common and easy to identify in the field. Nevertheless, models including only CWMs and divergence indices still have enough predictive power (cf. Table 1) and therefore can be used in those cases in which for theoretical or logistic reasons the idiosyncratic effects of particular species are to be excluded.

In synopsis, the stepwise modelling procedure applied here to explore the relative contribution of different functional diversity components – dominant trait values, divergence of single traits and multiple traits, effects of particular species –

in explaining the variation in C storage in Chaco forests showed that in all cases the combination of different components resulted in models with significantly larger explanatory power. The relative importance of the different components depended on the C stock analysed.

Very few other works have empirically tested different components of functional diversity in natural ecosystems (Thompson *et al.* 2005; Mokany, Ash & Roxburgh 2008; Schumacher & Roscher 2009), and even less work has been performed in woody ecosystems, which in general offer a complex picture. For example, in boreal forests of different composition originated by different natural fire regimes under similar climatic conditions, communities dominated by acquisitive trait values showed lower below-ground C storage than communities dominated by more conservative trait values (Jonsson & Wardle 2010; Wardle *et al.* 2012). In natural moist seasonal tropical forests, Ruiz-Jaen & Potvin (2011) reported C storage associated positively with plant height and leaf mass per area (the inverse of SLA) and negatively with the variety of values of these traits. In neighbouring plantations, in contrast, they found a negative association of C storage with plant height and leaf mass per area and a non-significant association with variety of values of these traits. Overall, these antecedents and our findings coincide in giving less support to the niche-complementarity hypothesis than to the mass ratio one, but also in highlighting the complexity of mechanisms operating in the field and their strong context dependence.

Conclusions

Our findings suggest that all three major components of plant functional diversity – the dominant trait values, the variety of trait values and the presence of particular species in the community – contribute to explain C storage at the ecosystem level.

The only dominant traits with strong explanatory power over C storage were stem traits, especially plant height. In contrast with other systems, we found no evidence of the association of C storage with leaf traits involved in well-documented resource-use syndromes. This may be a general trend of semi-arid forest ecosystems or a consequence of land use not changing the resource base of the plots strongly enough to result in important shifts in functional trait composition. This aspect merits further study, including combinations of contrasting climatic and soil resource conditions, as well as different land uses under the same abiotic conditions.

Our findings suggest that variety of trait values is a relevant component of functional diversity. However, because the association of a larger variety of trait values with C storage was significant, but always negative in the final models, we found no evidence in support of niche complementarity playing an important role in C storage capacity in these ecosystems.

The conclusions of this study, clear at the level of Chaco and other semi-arid woody ecosystems subjected to similar climate and land uses, are to be taken with caution when comparing ecosystems that markedly differ in resource base as a consequence of different water availability, length of the growing season or nutrient level in the soil.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Comparison of tree above-ground dry biomass estimates.

Table S1. Characterization of different ecosystem types.

Table S2. Summary of predictor and response variables.

Table S3. Dominant species and their trait values used to calculate community functional indices.

Table S4. Pairwise associations between C stocks and functional diversity components.

Table S5. Multivariate analysis of trait community weighted mean (CWM) of different sites, and their association with carbon storage.