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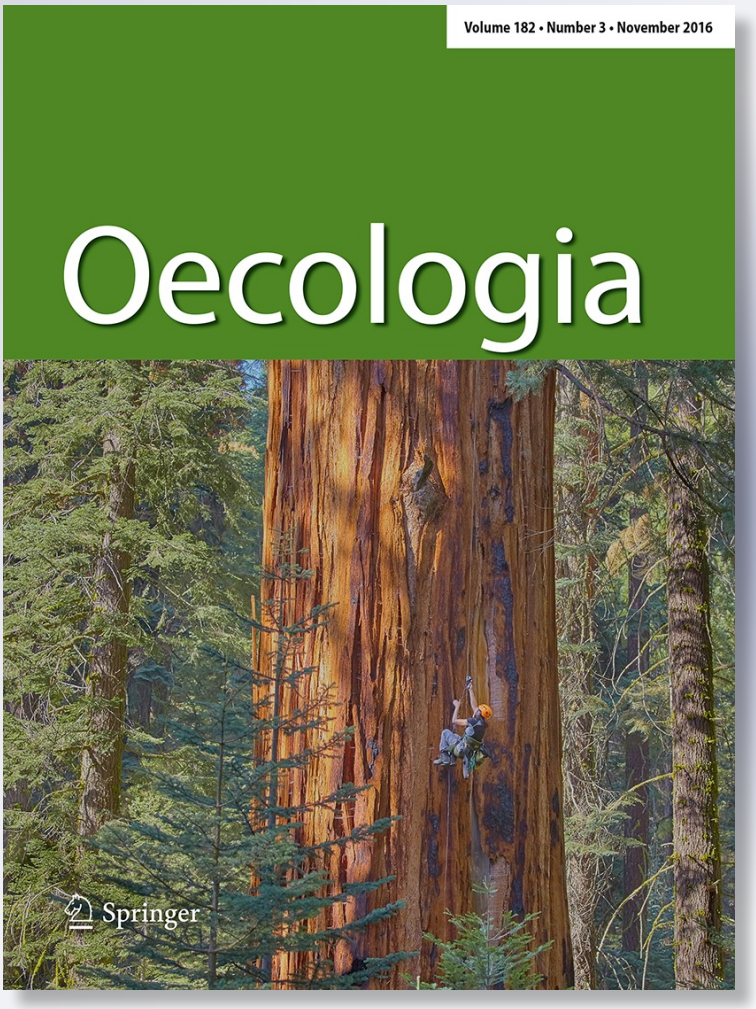

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COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Functional composition drives ecosystem function through multiple mechanisms in a broadleaved subtropical forest

Jyh-Min Chiang[1] · Marko J. Spasojevic[2] · Helene C. Muller-Landau[3] · I-Fang Sun[4] · Yiching Lin[1] · Sheng-Hsin Su[5] · Zueng-Sang Chen[6] · Chien-Teh Chen[7] · Nathan G. Swenson[8] · Ryan W. McEwan[9]

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Abstract Understanding the role of biodiversity (B) in maintaining ecosystem function (EF) is a foundational scientific goal with applications for resource management and conservation. Two main hypotheses have emerged that address B–EF relationships: niche complementarity (NC) and the mass-ratio (MR) effect. We tested the relative importance of these hypotheses in a subtropical old-growth forest on the island nation of Taiwan for two EFs: aboveground biomass (ABG) and coarse woody productivity (CWP). Functional dispersion (FDis) of eight plant functional traits was used to evaluate complementarity of resource use. Under the NC hypothesis, EF will be positively correlated with FDis. Under the MR hypothesis, EF will be negatively correlated with FDis and will be significantly influenced by community-weighted mean (CWM) trait values. We used path analysis to assess how these two processes (NC and MR) directly influence EF and may contribute indirectly to EF via their influence on canopy packing (stem density). Our results indicate that decreasing functional diversity and a significant influence of CWM traits were linked to increasing AGB for all eight traits in this forest supporting the MR hypothesis. Interestingly, CWP was primarily influenced by NC and MR indirectly via their influence on canopy packing. Maximum height explained more of the variation in both AGB and CWP than any of the other plant functional traits. Together, our results suggest that multiple mechanisms operate simultaneously to influence EF, and understanding their relative importance will help to elucidate the role of biodiversity in maintaining ecosystem function.

Keywords Complementarity hypothesis · Forest carbon dynamics · Functional diversity · Functional trait · Mass-ratio effect

Introduction

Understanding the relationship between biodiversity (B) and ecosystem function (EF) is an important goal in ecology (Díaz and Cabido 2001; Hooper et al. 2005; Tilman

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et al. 2014) that has taken on an added urgency due to the global loss of species (Rockström et al. 2009; Costello et al. 2013). Forests are important components of the global carbon cycle (Pan et al. 2011), and forest ecosystem function has often been characterized by assessing woody productivity (carbon flux) and standing biomass (carbon stock). Perhaps, the two most important and widely investigated B-EF hypotheses are niche complementarity (NC) and mass-ratio (MR) effects. The NC hypothesis proposes that increasing species richness increases resource-use efficiency and thereby enhances ecosystem function (Tilman 1997; Tilman et al. 2014). In contrast, the MR hypothesis proposes that EF is regulated by the dominant species in the community (Grime 1998). Under the MR hypothesis, variation in EF is explained largely by the functional identity of the dominant species, which can be estimated using the community-weighted mean of functional trait values (Garnier et al. 2004; Díaz et al. 2007; Mokany et al. 2008; Finegan et al. 2015). These two hypotheses are not necessarily mutually exclusive (Mokany et al. 2008) and understanding the relative contributions of NC and MR effects on ecosystem processes can inform forest management and conservation. Despite much effort in understanding the relative importance of these two mechanisms, uncertainties remain (Díaz and Cabido 2001; Hooper et al. 2005; Díaz et al. 2007). For example, stand age (Zhang and Chen 2015) and local spatial structure (Réjou-Méchain et al. 2014) have significant effects on the aboveground biomass and may generate uncertainty in understanding B–EF relationships. Moreover, the influence of environmental factors, such as soil resource availability, may generate spatial variation in forest productivity through variation in nutrient availability (LeBauer and Treseder 2008).

In forests, the investigation of B–EF relationships has focused almost exclusively on observational studies of extant spatial variation which have yielded mixed results. Paquette and Messier (2011) demonstrated a strong positive relationship between functional diversity and forest productivity in boreal forests, but not in adjacent temperate forest. Ruiz-Jaen and Potvin (2011) found that functional composition was a better predictor of carbon storage than was species richness, and the effects of species richness and functional diversity were negative. Chisholm et al. (2013) analyzed local variation within 25 temperate and tropical forests and discovered that the relationship of tree species richness to forest biomass and productivity varied among sites and with spatial grain, with a preponderance of significant positive relationships at small grains (0.04 ha) becoming mixed in direction and mostly insignificant at larger grains (1 ha). These conflicting patterns may be a result of a shift in the relative importance of NC and MR among sites, or may indicate that NC and MR operate simultaneously (Grace et al. 2016). Though experimental studies enable stronger inference in principle (e.g., Fargione et al. 2007), the resources required to manipulate compositions and the time required to observe treatment responses makes experiments more challenging in forests (but see Potvin et al. 2011).

Assuming that functional niche differentiation underlies NC, functional diversity indices should outperform taxonomic diversity indices, such as species richness in predicting EF (Mason et al. 2005; Villéger et al. 2008; Laliberté and Legendre 2010). Functional traits have been linked to forest tree abundance dynamics (Li et al. 2015) and competition and co-existence (Kunstler et al. 2016). Particularly, functional dispersion (FDis), which quantifies the mean distance in multidimensional trait space of individual species to the centroid of all species, can be conceptualized as the degree of trait dissimilarity among species within a community (Mason et al. 2005; Laliberté and Legendre 2010). Specifically, higher functional dispersion suggests low-resource competition as a result of high niche differentiation (Laliberté and Legendre 2010; Mason et al. 2005). Thus, if NC drives EF, then ecosystem functioning should increase with increasing FDis. Alternatively, the MR effect suggests that EF is regulated by the dominant species in the community and is weakly influenced by less abundant species. Thus, if MR drives EF, then ecosystem functioning should be more strongly influenced by community-weighted mean (CWM) trait values and negatively related to FDis, as the dominant trait value (not the diversity of traits) drives EF.

In this study, we used path analysis to investigate how the functional diversity of a tree community is related to ecosystem functions in a taxonomically and functionally diverse subtropical old-growth forest in Taiwan. We analyzed how spatial variation in two ecosystem functions (EF)—aboveground biomass (AGB) and coarse woody productivity (CWP)—were related to the bottom–up effect of environmental conditions (soil properties), stem density, functional dispersion (FDis), and CWM trait values of the tree community. We analyzed eight putatively important plant functional traits which are known to impact the survival and growth of trees at our study site (Iida et al. 2014). We evaluated the following three hypotheses: H_1 EF is significantly positively related to tree functional diversity (FDis), in accordance with niche complementarity (NC) and consistent with the previous findings of a positive relationship between tree species richness and AGB at this site (McEwan et al. 2011a). H_2 In accordance with the mass-ratio hypothesis (MR), EF is strongly related to the functional identity of the community as measured by CWM trait values and negatively related to FDis (Díaz et al. 2007). H_3 The effects of NC and MR on EF are mediated by stem density (canopy packing), because greater stem density is associated with both more diversity and more biomass and productivity (Chisholm et al. 2013).

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Methods

Study site

This study was conducted at the Fushan Forest Dynamics Plot (hereafter Fushan; 24°45′N, 121°33′E) in northern Taiwan. Climate at the site is subtropical with an average annual temperature and precipitation of 18.2 °C and 4271 mm, respectively (Su et al. 2007). Fushan is an old-growth forest that has been protected by the aborigines for centuries (Bureau of Aborignial Affairs 1911). It is also susceptible to frequent typhoon strikes with a mean of 0.74 typhoons per year between 1951 and 2005 (Lin et al. 2011; Yao et al. 2015; Chi et al. 2015). Much of the precipitation at Fushan is from the monsoon in the winter and frequent typhoons in the summer. Elevation in Fushan ranges from 600 to 733 m above sea level.

The 25 ha (500 m × 500 m) Fushan plot was censused in 2003–2004 and 2008–2009 by the Taiwan Forestry Research Institute, the Forestry Bureau of Taiwan, and the National Taiwan University. The 25 ha plot was divided into a grid of 625 20 m × 20 m quadrats. Following Condit (1998), all woody stems with diameter at breast height (DBH) ≥1 cm were measured, tagged, mapped, and identified to species. A total of 110 woody species, representing 67 genera and 39 families, were documented (Su et al. 2007). Dominant species include *Limlia uraiana, Castanopsis cuspidata, Engelhardtia roxburghiana, Pyrenaria shinkoensis,* and *Meliosma squamulata* (Su et al. 2007).

Each 0.04 ha quadrat (20 m × 20 m) was treated as an observational unit in our analyses. We included only stems with DBH ≥5 cm (90 woody species), because these are responsible for almost all coarse woody productivity and aboveground biomass. The relative basal area of trees ≥5 cm DBH of each species in each quadrat was calculated based on the second census to construct a community composition matrix (quadrat by species), which was then used as weighing factors for the calculation of functional diversity.

Soil properties

Soil samples were collected from 80 cells that ranged in size from 40 m × 40 m to 80 m × 100 m. For each cell, four soil samples were collected, mixed, air-dried, and sieved with 2 mm mesh size before physical and chemical analyses. Nine soil variables, including soil pH, electrical conductivity, organic carbon, available N, available P, available K, soil exchangeable Ca, Mg, and Na content, were analyzed for each cell (Shen et al. 2013). The geostatistical software (Surfer 7.0) was used to produce the soil distribution map for the plot, and then, Kriging was used to estimate soil properties for each 20 m × 20 m quadrat. To account for collinearity among soil variables, the first three principal component axes of the quadrat-level soil variables that explained most variations were used for the subsequent analyses. Principle component 1 explained 38.7 % of variation and represents a gradient from areas with high available K, electrical conductivity, organic carbon, Ca, and Mg (low PC1 scores) to areas with low amounts of these soil properties. Principle component 2 represents an axis of variation describing a shift from areas with high pH (low PC2 scores) to areas with low pH. Principle component 3 represents a gradient from areas with high available P (low PC3 scores) to areas with high available N and Na (high PC3 scores; loadings shown in Electronic Supplemental Material Table A1). Principle components 2 and 3 explain 18.6 and 13.6 % of variation, respectively.

Functional traits, functional identity, and functional diversity

Mean functional trait values for each species were calculated based on measurements of the six largest individuals of each species in the summer (June to August) of 2009. Tree heights were measured using measuring poles (for tree height ≤15 m) or laser rangefinders (for tree height >15 m), and species maximum tree height (H_{max}) was estimated as the mean height of these six largest individuals. Crown radii were measured in the eight principal directions (N, NE, E, SE, S, SW, W, and NW) from the approximate centre to the edge of the crown, and crown area was calculated as $\pi \times CR^2$ (CR: the geometric mean of crown radii). Residuals of the linear function between crown area and basal area of individual stems (CABA) were calculated, and the mean residuals were calculated for each species as a measure of the spread of the crown after correcting for tree size—higher values are expected to be associated with higher susceptibility to wind damage and higher shade tolerance.

Leaf traits were measured on three sun leaves collected from each of the focal individuals. Collected leaves were immediately placed in a cool box and covered with wet tissue. On the same day of leaf collection, petioles and rachis (of compound leaves) were removed and fresh leaf mass was measured. Leaf area (LA; m^2) for each leaf was measured using the software Image J (NIH Image; http://rsb.info.nih.gov/ij/) applied to a scanned image of the leaf beside a 5 cm scale bar. Each leaf was dried to a constant weight at 70 °C and then weighed. We calculated leaf mass per area (LMA; g m^{-2}) and leaf dry matter content (LDMC; leaf dry mass/fresh mass) for each leaf. Mass-based concentrations of organic leaf nitrogen (LeafN, %) and phosphorous (LeafP, %) were determined by two microplate methods

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(Huang et al. 2011; Iida et al. 2014). LA was highly skewed and, therefore, log transformed for subsequent analyses.

Wood density (WD; strictly wood specific gravity; g cm^{-3}) values for each species were based on wood samples from five individuals from outside the boundaries of the permanent plot (minimum DBH = 10 cm). Wood cores were collected with an increment borer in the winter of 2010 (from December 2010 to January 2011) and broken into 5 mm segments in the lab. Fresh volume for each segment was determined using the water displacement method, and dry weight was measured after oven-drying at 80 °C. Wood density for each segment was calculated by dividing dry weight by fresh volume, and wood density for each tree was calculated as the weighted average over segments, weighting by the stem cross-sectional area in each successive concentric ring (Wright et al. 2010). The pairwise trait relationships are shown in Electronic Supplemental Material Fig. A1.

Despite considerable effort, we were unable to obtain trait data for all species in our study area. Thus, our calculations of functional diversity were based on 80 species for which we had data on three or more traits measured per species, as we felt that we would not accurately capture a species' functional trait strategy with fewer than three traits. (Electronic Supplemental Material Table A2). These 80 species comprised 95 % of the basal area in the whole plot, and between 46 and 100 % of the basal area in individual quadrats. To minimize the potential effect of missing trait values, we further excluded any quadrats with less than 80 % of relative basal area represented by the 80 species for which we had trait data, leaving 606 out of 625 quadrats for the statistical analyses. We calculated FDis for each trait individually, as the mean distance of each species in trait space to the centroid of all species using the dbFD function of FD package in R (Laliberté and Legendre 2010), with tree species weighted by their respective relative basal area. FDis is statistically independent of species richness (Laliberté and Legendre 2010). Here, we focus on individual trait analyses, because ecological processes may be masked by multivariate trait indices that integrate traits with potentially opposing influences on our response variables (Spasojevic and Suding 2012). Community-weighted means (CWM) of each trait for each quadrat were calculated based on basal-area-weighted averages to represent functional identity (FI) of the selected 80 species.

Aboveground biomass and coarse woody productivity

Aboveground biomass for each individual stem was estimated from DBH (cm), tree height (m), and wood density (ρ) using a generalized (mixed species) allometric equation developed for tropical moist forests (Chave et al. 2005):

$$\mathrm{AGB_{stem}} = \exp\left(-2.977 + \ln\left(\rho \times \mathrm{DBH}^2 \times H\right)\right). \quad (1)$$

Tree height of each individual stem was estimated by a locally derived DBH-height allometric equation (McEwan et al. 2011a), and wood density was assigned based on species identity. $\mathrm{AGB_{stem}}$ estimated by this equation had previously been locally validated with 96 felled trees (McEwan et al. 2011a).

AGB for each 20 m × 20 m quadrat (hereafter AGB; Mg ha^{-1}) was calculated by summing AGB of all stems in each quadrat. AGB of the second census (2008–2009) was used for statistical analyses. Based on the two censuses, coarse woody productivity (CWP; Mg ha^{-1} $year^{-1}$) for each quadrat was calculated as the sum of AGB increments of surviving stems and AGB of new stems, divided by the duration of the census interval. Stems with AGB decrements were assumed to have zero CWP, because CWP for individual tree cannot, by definition, be negative.

Statistical analysis

We estimated spatial autocorrelation in CWP and AGB by semivariances (Cressie 1993). Monte Carlo simulations based upon spatial randomness were applied to construct 95 % confidence intervals of semivariances (Diggle and Ribeiro 2007). Spatial autocorrelation only affects tests of correlation between response and explanatory variables when both variables are spatially autocorrelated (Legendre et al. 2002). Having found no spatial autocorrelation in the response variables, we then analyzed the univariate relationships among EF variables (CWP and AGB), FDis, CWM trait values, stem density, and soil factors (the first three principal components of soil variables) to screen our data (i.e., test for non-linear relationships among our variables) and to aid in the interpretation of our results. We tested for both linear and quadratic relationships for each response measure and selected the best fit using Akaike Information Criteria (Burnham and Anderson 2004). Prior to analysis, CWP and AGB were log transformed to approach linear relationships with potentially related independent variables. We then used path analysis to investigate links among FDis, CWM trait values, soil variables, stem density, and each measure of EF. We built an initial model (Fig. 1) that included the direct effects of soils, stem density, NC and MR on EF and the indirect effect of soils via their influence on stem density, NC, and MR, as well as the indirect effects of NC and MR via their influence on stem density. In our model, we only considered the bottom–up effect of soil resources on FDis, CWM trait values, and stem density. We acknowledge that these properties of the tree community likely also influence soil resource availability, but such an analysis is beyond the scope of this study and would require more dynamic measurements of soil resource availability, which we presently do not have. Moreover, here,

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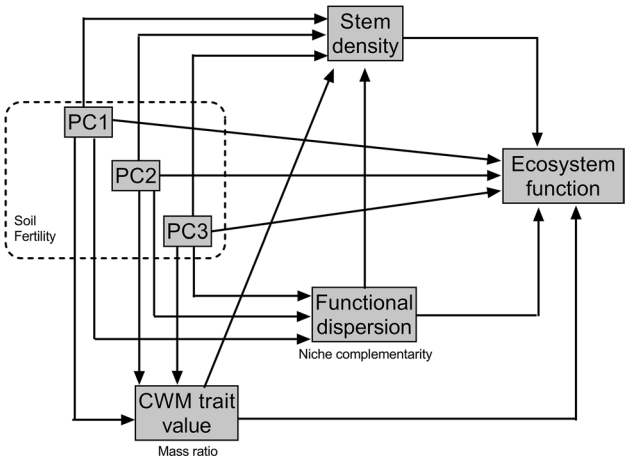

Fig. 1 General form of the path analysis used to evaluate how soil fertility (PC1-3: the first three axes from a principle components analysis), stem density, community-weighted mean (CWM) trait values, and functional dispersion (FDis) of tree communities is related to ecosystem function

we focus on the influence of FDis on stem density—as opposed to the influence of stem density on FDis—as we are interested in testing a specific hypothesis about the role of niche complementarity (we use FDis as a proxy for niche complementarity) on stem density and ecosystem function.

For each model, we first assessed model fit with Chi-square (χ^2) tests, root mean square error of approximation (RMSEA), and goodness-of-fit index (GFI). χ^2 values associated with a P value >0.05 (suggesting that observed and expected covariance matrices are not different), RMSEA <0.05, and GFI >0.95 indicate a good model fit (Kline 2010). We then used the "modindices" function to find paths whose removal from the model would result in the biggest improvement in the overall Chi-square value until we found the model with the lowest Akaike information criterion (AIC) score that had a good model fit. Path analysis was conducted using the Lavaan package (Rosseel 2012) implemented in R (R Core Team 2014). In our results (Figs. 1, 2), non-significant pathways (arrows) have been removed (as compared to the initial model). It is important to note that when interpreting a path analysis, consistency between our statistical model and data does not mean that our interpretations are correct, only that the data are consistent with our interpretations (McCune and Grace 2002).

Results

Spatial distribution of CWP and AGB

Coarse woody productivity (CWP) ranged from 0.62 to 13.94 Mg ha^{-1}year^{-1} among 625 quadrats (Electronic Supplemental Material Fig. A2) with a median of 3.54 Mg ha^{-1}year^{-1}. Aboveground biomass (AGB) ranged from 19.7 to 672.8 Mg ha^{-1} across quadrats with a median of 168 Mg ha^{-1}. Low AGB tended to be found on a topographic peak in the southwest quadrant of the plot (Electronic Supplemental Material Fig. A2). No statistically significant spatial autocorrelation was detected for CWP or AGB.

Relative importance of soils, stem density, functional dispersion, and CWM trait values on ecosystem functioning

AGB and CWP showed varied linear relationships with the three soil variables, stem density, and FDis and CWM trait values for each trait (Electronic Supplemental Material Table A3).

Aboveground biomass

All eight models were found to have a close fit to the data (Table 1), but varied in the amount of variance in aboveground biomass explained (r^2 between 0.14 and 0.51). For all eight plant functional traits, FDis was negatively related to AGB and there was a significant effect of CWM trait values. Stem density exhibited a direct influence on AGB in all eight models (Fig. 2). However, for all traits except CABA and $H_{max,}$ we found an indirect effect of NC on AGB via stem density. There were direct effects of the three soil factors on AGB in a few instances (Fig. 2). In our model with LA, we found that all three PC axes directly influenced AGB; in our model for LDMC, PC2 (pH) directly influenced AGB; for CABA PC3 (P, N, Na) directly influenced AGB; for LeafP both PC2 (pH) and PC3 (P, N, Na) directly influenced AGB. For all other traits, the effect of soils of AGB was mediated by a combination of stem density, CWM traits, and FDis, suggesting that the soil variables in these models largely influence AGB indirectly through their influence of plant functional traits or stem density.

The amount of variation in AGB explained by the eight traits varied (Fig. 2). While the general structure of all eight models was relatively similar, the models with H_{max} and LA were the only models, where the total effect of CWM trait values contributed more to AGB than either FDis or stem density (Table 2). However, the model with H_{max} explained 51 % of the variation in AGB, while the model with LA only explained 16 %. The models for LeafP and WD explained little of the variation in AGB (19 and 14 %, respectively) and CWM trait contributed less to AGB than FDis or stem density, suggesting that these traits may not be as informative for assessing B–EF relationships for AGB in this forest. The models with LMA, LDMC, and CABA

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Table 1 Goodness-of-fit measures—Chi-square (χ^2) tests, root mean square error of approximation (RMSEA), and goodness of fit index (GFI)—for each of the 16 path analyses, testing how tree community functional diversity is related to ecosystem functions

EF	Trait	χ^2	*df*	*P* value	RMSEA	GFI	R^2
AGB	LA	0.108	1	0.743	0.000	0.999	0.16
	LMA	1.324	1	0.250	0.023	0.999	0.26
	LDMC	0.966	2	0.617	0.000	1.000	0.21
	CABA	1.584	2	0.453	0.000	0.999	0.27
	LeafN	0.059	1	0.809	0.000	1.000	0.37
	LeafP	1.329	4	0.249	0.023	0.999	0.19
	WD	1.833	1	0.176	0.037	0.999	0.14
	H_{max}	1.149	3	0.765	0.000	0.999	0.51
CWP	LA	0.108	1	0.743	0.000	0.999	0.19
	LMA	1.324	1	0.250	0.023	0.999	0.18
	LDMC	0.966	2	0.617	0.000	1.000	0.19
	CABA	0.151	1	0.698	0.000	1.000	0.19
	LeafN	0.059	1	0.809	0.000	1.000	0.20
	LeafP	1.723	2	0.423	0.000	0.999	0.18
	WD	1.833	1	0.176	0.037	0.999	0.21
	H_{max}	1.149	3	0.765	0.000	0.999	0.25

χ^2 values associated with a *P* value >0.05 (suggesting that observed and expected covariance matrices are not different), a RMSEA <0.05, and a GFI >0.95 indicate a good model fit (Kline 2010). Traits include leaf area (LA; cm^2 and log transformed), leaf mass per area (LMA; g m^{-2}), leaf dry matter content (LDMC, % fresh mass), residuals of the linear function between crown area and basal area of individual stems (CABA), leaf nitrogen content (LeafN; % dry mass), leaf phosphorus content (LeafP; % dry mass), wood density (WD; g cm^{-3}), and maximum height (H_{max}; meter). Ecosystem functions (EF) include aboveground biomass (AGB, Mg ha^{-1}) and coarse woody productivity (CWP, Mg ha^{-1} $year^{-1}$)

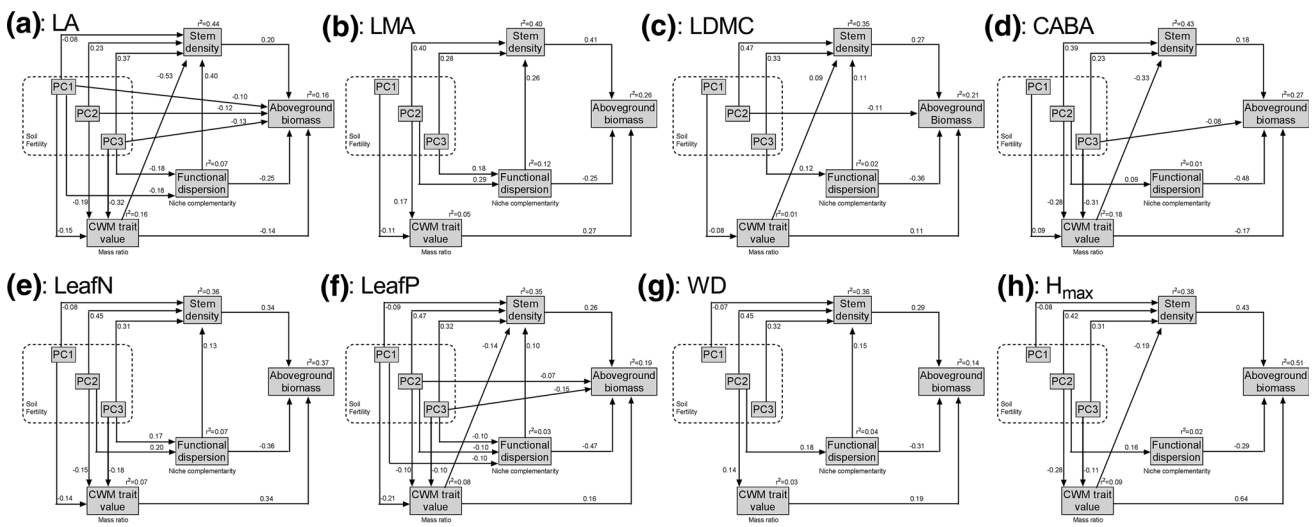

Fig. 2 Path analysis testing the relative importance of niche complementarity, mass ratio, and stem density on aboveground biomass—including individual models for **a** leaf area (LA), **b** leaf mass per area (LMA), **c** leaf dry matter content (LDMC), **d** residuals of the linear function between crown area and basal area of individual stems (CABA), **e** leaf nitrogen content (LeafN), **f** leaf phosphorus content (LeafP), **g** wood density (WD), and **h** maximum height (H_{max}). *CWM* community-weighted mean trait values. PC1-3 = soil fertility based on the first three axes of a principle components analysis of ten soil variables. Path coefficients are standardized prediction coefficients (Grace and Bollen 2005). Pathways not found to be influential (non-significant $P > 0.05$) are removed

all explained moderate amounts of the variation in AGB (26, 21, and 27 %, respectively), but for all of these traits, stem density contributed more to AGB than CWM traits as well. The model for LeafN explained 34 % of the variation in AGB and stem density and CWM trait values contributed equally to AGB.

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Table 2 Direct, indirect and total standardized effects (based on path analysis) of the six predictor variables on aboveground biomass

Predictor	Pathway to aboveground biomass	Effect (pathway coefficient)							
		LA	LMA	LDMC	CABA	LeafN	LeafP	WD	H_{max}
FDis	Direct	−0.25	−0.25	−0.36	−0.48	−0.36	−0.47	−0.31	−0.29
	Indirect through stem density	0.08	0.11	0.03	NS	0.04	0.03	0.04	NS
	Total effect	−0.17	−0.14	−0.33	−0.48	−0.32	−0.44	−0.27	−0.29
CWM traits	Direct	−0.14	0.27	0.11	−0.17	0.34	0.16	0.19	0.64
	Indirect through stem density	−0.11	NS	0.02	−0.06	NS	−0.04	NS	−0.08
	Total effect	−0.25	0.27	0.13	−0.23	0.34	0.12	0.19	0.56
Stem density	Direct	0.20	0.41	0.27	0.18	0.34	0.26	0.29	0.43
PC1	Direct	−0.10	NS	NS	NS	NS	NS	NS	NS
	Indirect through FDis	0.05	NS	NS	NS	NS	0.05	NS	NS
	Indirect through CWM traits	0.02	−0.03	0.02	0.02	−0.05	−0.05	NS	NS
	Indirect through stem density	−0.02	NS	−0.02	NS	−0.03	−0.02	−0.02	−0.03
	Indirect through FDis and stem density	−0.02	NS	NS	NS	NS	−0.003	NS	NS
	Indirect through CWM traits and stem density	0.02	NS	−0.002	−0.01	NS	0.01	NS	NS
	Total effect	−0.05	−0.03	0.002	0.01	−0.07	−0.02	−0.02	−0.03
PC2	Direct	−0.12	NS	−0.11	NS	NS	−0.07	NS	NS
	Indirect through FDis	NS	−0.07	NS	−0.04	−0.07	0.05	−0.06	−0.05
	Indirect through CWM trait value	0.03	0.05	NS	0.05	−0.05	0.03	0.03	−0.18
	Indirect through stem density	0.05	0.16	0.13	0.07	0.15	0.05	0.13	0.18
	Indirect through FDis and stem density	NS	0.03	NS	NS	0.01	−0.003	0.01	NS
	Indirect through CWM traits and stem density	0.02	NS	NS	0.02	NS	0.02	NS	0.02
	Total effect	−0.03	0.17	0.02	0.09	0.04	0.07	0.11	−0.02
PC3	Direct	−0.13	NS	NS	−0.08	NS	−0.15	NS	NS
	Indirect through FDis	0.05	−0.05	−0.04	NS	−0.06	0.07	NS	NS
	Indirect through CWM trait value	0.04	NS	NS	0.05	−0.06	−0.03	NS	−0.07
	Indirect through stem density	0.07	0.11	0.09	0.04	0.11	0.08	0.09	0.13
	Indirect through FDis and stem density	−0.01	0.02	0.003	NS	0.01	−0.004	NS	NS
	Indirect through CWM traits and stem density	0.03	NS	NS	0.02	NS	0.01	NS	0.01

Effects (pathway coefficients) describe the relative strength of the relationship between a given predictor variable and ecosystem function. Positive values indicate a positive relationship, while negative values indicate a negative relationship

See Table 1 for trait abbreviations

FDis functional dispersion, *CWM* community-weighted mean trait values, *PC1-3* soil fertility based on the first three axes of a principle components analysis of ten soil variables, *NS* non-significant relationships

Coarse woody productivity

All eight models were found to have a close fit to the data (Table 1), but varied in the amount of variance in CWP explained (r-squared between 0.18 and 0.25). FDis was negatively related to CWP for four of the eight traits (LDMC, leafP, WD, and H_{max}), while for $H_{max,}$ both FDis and CWM trait values significantly influenced CWP (Fig. 3). LeafN was the other trait for which CWM trait values influenced CWP. Together, these patterns suggest that neither NC nor MR contribute strongly to CWP in this forest. On the other hand, in all eight models, we found a direct influence of stem density on CWP (Fig. 3). For all traits except CABA and H_{max}, there was an indirect effect of FDis on CWP via stem density. For LDMC, CABA, leafP, and $H_{max,}$ there was an indirect effect of CWM trait values on CWP via stem density.

In all eight models PC1 (available K, electrical conductivity, organic carbon, Ca, and Mg) directly influenced CWP, while PC2 (pH) and PC3 (P, N, Na) had no direct effect (Fig. 3). However, PC2 and PC3 did indirectly effect CWP by influencing stem density, CWM trait values, and FDis, suggesting that pH, P, N, and Na may only influence CWP indirectly through their influence on plant functional traits or stem density.

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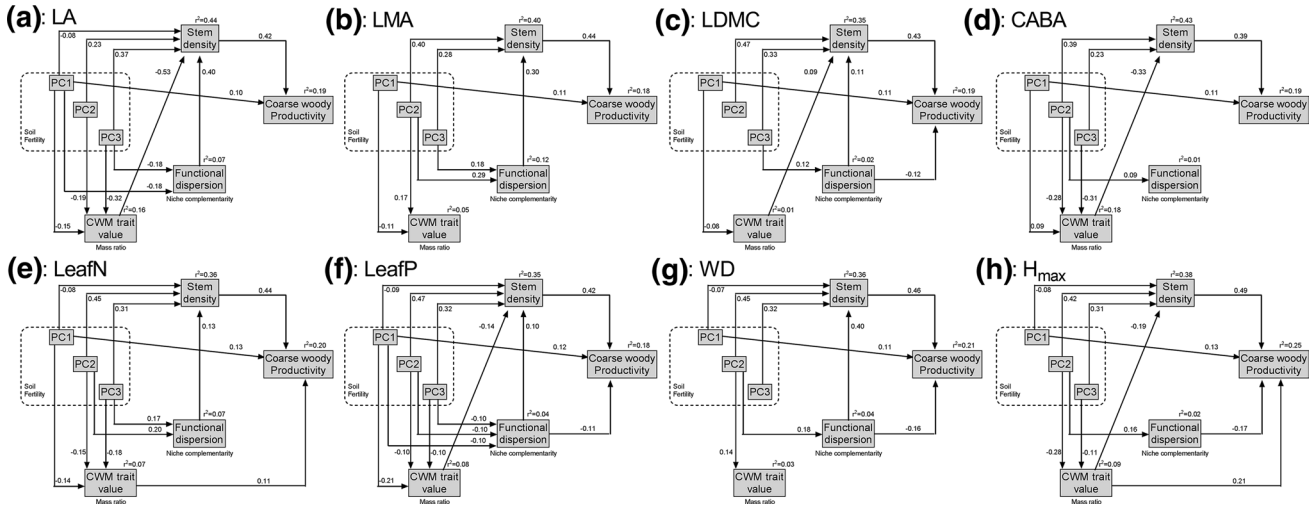

Fig. 3 Path analysis testing the relative importance of niche complementarity, mass ratio, and stem density on coarse woody productivity—including individual models for **a** leaf area (LA), **b** leaf mass per area (LMA), **c** leaf dry matter content (LDMC), **d** residuals of the linear function between crown area and basal area of individual stems (CABA), **e** leaf nitrogen content (leafN), **f** leaf phosphorus content (LeafP), **g** wood density (WD), and **h** maximum height (H_{max}). *CWM* community-weighted mean trait values. PC1-3 = soil fertility based on the first three axes of a principle components analysis of ten soil variables. Path coefficients are standardized prediction coefficients (Grace and Bollen 2005). Pathways not found to be influential (non-significant $P > 0.05$) are removed

The amount of variation in CWP explained by the eight traits varied (Fig. 3), with H_{max} explaining the most (25 %) and LMA and LeafP explaining the least (18 %). These models were more variable than AGB, with some having no direct effects of CWM trait values or FDis on CWP: LA, LMA, and CABA. In no model, did the total effect of CWM trait values or FDis contribute more to CWP than stem density (Table 3), suggesting that these traits may not be particularly informative for assessing B–EF relationships for CWP in this forest.

Discussion

Multiple mechanisms have been shown to operate simultaneously and affect community dynamics and ecosystem function (Mokany et al. 2008; McEwan et al. 2011b; Grace et al. 2016). Data from our subtropical forest study system indicate, specifically, that in our subtropical forest study area, B–EF relationships are due to simultaneous influences of niche complementarity (NC) and mass-ratio (MR) effects. Functional identity (CWM trait values) was closely linked to EF, while functional dispersion (FDis) was negatively associated with EF suggesting that the dominance of species with particular functional traits led to increasing EF which is indicative of MR effects (Grime 1998). We also found that NC indirectly influenced EF via its influence on stem density; FDis had a positive effect on EF by increasing stem density, suggesting that NC still contributes to EF in these forests. Moreover, we also found that MR indirectly influenced EF via its influence on stem density for CABA and H_{max}, suggesting that MR effects operate through both direct and indirect mechanisms. Together, our results support the idea that the MR and NC hypotheses are not mutually exclusive (Mokany et al. 2008) and highlight the importance of examining the direct and indirect effects of these processes when seeking to understand EF.

Our results are inconsistent with NC as the primary driver of EF and refute H_1 that functional diversity measures would be positively related to EF in this diverse subtropical forest. Specifically, we found a negative direct relationship between functional dispersion (FDis) and AGB for all eight traits and either a negative (LDMC, LeafP, WD, and H_{max}) or no relationship (LA, LMA, CABA, and LeafN) with CWP. The concept of NC as a driver of EF is heuristically compelling, ecologically reasonable, and supported by simulation models, experiments, and some observational studies (e.g., Tilman 1999; Cardinale et al. 2007; Fargione et al. 2007; Morin et al. 2011). For instance, Barrufol et al. (2013) found that tree species richness was positively related to biomass accumulation during tropical forest succession. Tree size inequality, which is related to tree species diversity, has been linked with increased biomass in boreal forests (Zhang and Chen 2015). Even so, it is far from clear that the NC-EF paradigm holds for all ecosystems and varying results have been found in forests (Reiss et al. 2009; Paquette and Messier 2011; Ruiz-Jaen and Potvin 2011). While the previous work at our site suggested a positive relationship between tree species richness and EF (McEwan et al. 2011a), taxonomic measures, such

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Table 3 Direct, indirect, and total standardized effects (based on path analysis) of the six predictor variables on coarse wood productivity

Predictor	Pathway to coarse woody production	Effect (pathway coefficient)							
		LA	LMA	LDMC	CABA	LeafN	LeafP	WD	H_{max}
FDis	Direct	NS	NS	−0.12	NS	NS	−0.11	−0.16	−0.17
	Indirect through stem density	0.17	0.13	0.05	NS	0.06	0.04	0.18	NS
	Total effect	0.17	0.13	−0.07	0.00	0.06	−0.07	0.02	−0.17
CWM traits	Direct	NS	NS	NS	NS	0.11	NS	NS	0.21
	Indirect through stem density	0.22	NS	0.04	−0.13	NS	−0.06	NS	−0.09
	Total effect	0.22	0.00	0.04	−0.13	0.11	−0.06	0.00	0.12
Stem density	Direct	0.42	0.44	0.43	0.39	0.44	0.42	0.46	0.49
PC1	Direct	0.10	0.11	0.11	0.11	0.13	0.12	0.11	0.13
	Indirect through FDis	NS	NS	NS	NS	NS	−0.01	NS	NS
	Indirect through CWM traits	NS	NS	NS	NS	−0.02	NS	NS	NS
	Indirect through stem density	−0.03	NS	NS	NS	−0.04	−0.04	−0.03	−0.04
	Indirect through FDis and stem density	−0.03	NS	NS	NS	NS	−0.004	NS	NS
	Indirect through CWM traits and stem density	0.03	NS	−0.003	−0.01	NS	0.01	NS	NS
	Total effect	0.07	0.11	0.11	0.10	0.08	0.08	0.08	0.09
PC2	Direct	NS	NS	NS	NS	NS	NS	NS	NS
	Indirect through FDis	NS	NS	NS	NS	NS	−0.01	−0.03	−0.03
	Indirect through CWM trait value	NS	NS	NS	NS	−0.02	NS	NS	−0.59
	Indirect through stem density	0.10	0.18	0.20	0.15	0.20	0.20	0.21	0.21
	Indirect through FDis and Stem density	NS	0.04	NS	NS	0.01	−0.004	0.03	NS
	Indirect through CWM traits and stem density	0.04	NS	NS	0.04	NS	0.006	NS	0.03
	Total effect	0.14	0.21	0.20	0.19	0.19	0.19	0.21	−0.38
PC3	Direct	NS	NS	NS	NS	NS	NS	NS	NS
	Indirect through FDis	NS	NS	−0.01	NS	NS	−0.01	NS	NS
	Indirect through CWM trait value	NS	NS	NS	NS	−0.02	NS	NS	−0.02
	Indirect through stem density	0.16	0.12	0.14	0.09	0.14	0.13	0.15	0.15
	Indirect through FDis and stem density	−0.03	0.02	0.006	NS	0.01	−0.004	NS	NS
	Indirect through CWM traits and stem density	0.07	NS	NS	0.04	NS	0.006	NS	0.01
	Total effect	0.20	0.15	0.13	0.13	0.126	0.13	0.15	0.14

Effects (pathway coefficients) describe the relative strength of the relationship between a given predictor variable and ecosystem function. Positive values indicate a positive relationship, while negative values indicate a negative relationship

See Table 1 for trait abbreviations

FDis functional dispersion, *CWM* community-weighted mean trait values, *PC1-3* soil fertility based on the first three axes of a principle components analysis of ten soil variables, *NS* non-significant relationships

as species richness, do not account for the fact that some species may be functionally redundant (Loreau 2004). Our results reinforce the importance of considering functional, as well as taxonomic diversity when analysing B–EF relationships (Díaz and Cabido 2001).

The MR hypothesis predicts that ecosystem properties should be largely determined by the characteristics of the dominant species within a community (Grime 1998) and we expected to see strong relationships between functional identity (CWM trait values) and EF if the MR hypothesis was supported. We found that CWM trait values for all eight traits were directly related to AGB and that CWM trait values for leafN and H_{max} were directly related to CWP. Similar findings were reported by Hooper and Vitousek (1997) who noted that the identity of particular functional groups present, not functional diversity per se, was the best predictor of aboveground biomass in serpentine grasslands. Moreover, Finegan et al. (2015) found a strong MR effect on aboveground biomass storage and increment in Bolivian, Costa Rican, and Brazilian tropical

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forests. If individual traits are strongly related to a particular capacity or function of interest, increasing functional diversity could dilute the efficacy of the local plant community in performing that function.

We found evidence that variation in stem density serves as a mechanism by which both NC and MR hypotheses can operate simultaneously and indirectly in a forest to influence EF. Forest communities with higher stem density are generally associated with higher diversity and greater biomass (Chisholm et al. 2013). Supporting this idea, we found a strong positive relationship between stem density and both CWP and AGB in all our models. These analyses also revealed consistent evidence of a positive relationship between FDis and stem density. Specifically, these models suggest that increasing FDis in key traits is associated with increased stem density and an increase in both AGB and CWP. The relationship between diversity and stem density may be linked with "canopy packing" which optimizes space utilization and, in our example, may lead to increased local biomass. Zhang and Chen (2015) demonstrated that diversity is linked with increased biomass due to increasing tree size inequality in a boreal forest. Similarly, Jucker et al. (2015) found that canopy packing was strongly associated with species richness in European permanent forest plots. Our results suggest that canopy packing may influence both AGB and CWP and that both NC and MR effects may contribute to EF indirectly by influencing canopy packing. Interestingly, we found a positive relationship between FDis and stem density suggesting that NC was an important driver of stem density. There were only two traits (CABA and H_{max}), where we found support for MR influencing stem density (a negative or no relationship between FDis and stem density and a significant relationship between CWM trait values and stem density). While these patterns suggest that the MR effect may also indirectly influence EF by affecting stem density, taken as a whole our results suggest that NC may be a strong indirect driver of EF, while MR primarily influences EF directly.

The eight functional traits in our analysis differed in their influence on EF. In particular, H_{max} had the strongest influence on EF (largest path coefficients) and the models with H_{max} explained the most variation in AGB ($r^2 = 0.51$) and CWP ($r^2 = 0.26$) as compared to the other traits. Similarly, Conti and Díaz (2013) found that plots with low variation in tree height were associated with higher carbon storage, while increasing variation in tree height was associated with lower EF. For the other functional traits, we found that LA, LeafP, WD, and LDMC were relatively weak predictors of AGB (model $r^2 = 0.16$, 0.19, 0.14, and 0.21, respectively), while LMA, CABA, and LeafN performed better (model $r^2 = 0.26$, 0.27, and 0.37, respectively). In contrast, none of the eight traits were particularly strong predictors of CWP.

In summary, our results provide a novel perspective on the B–EF relationship in tropical forests on the island nation of Taiwan in which both MR and NC are linked to forest biomass and productivity. Functional diversity was negatively associated with EF, as would be expected if greater diversity was associated with a higher frequency of inferior trait values. However, we found an indirect, positive link between FDis and stem density suggesting that complementarity could be an indirect driver of EF in these forests. Functional identity (CWM trait values) was closely linked to EF in some models, and was particularly strong for maximum tree height. This results suggests that, in landscape positions, where trees are protected from disturbances (such as wind; McEwan et al. 2011a), the dominance of species with traits associated with greater tree height is associated with increased EF. Interestingly, we also found significant links between CWM trait values and stem density. These results suggest that MR effects operate through multiple mechanisms, and further, that stem density is a mechanism through which MR and NC may simultaneously influence EF. Future work that address B–EF in high-diversity systems, where stem density varies widely, offers promise for elucidating the mechanisms linking various forms of biological diversity to ecosystem function.

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Author contribution statement JMC conceived and formulated the research idea. JMC, MJS, HCM, YL, and NGS developed the analytical procedures. MJS conducted path analysis. IFS and SHS maintain the study plot and census data. JMC, IFS, ZSC, and CTC provided functional trait and soil data. JMC and RWM wrote the first manuscript draft and others commented and contributed to the text.

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