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RESEARCH PAPER

Productivity as related to diversity and age in planted versus natural forests

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ABSTRACT

Aim Little is known about the performance of plantations relative to natural forests of the same climate zone and age. China has more plantations than any other country as a consequence of massive afforestation efforts. We use data from China to comparatively examine tree biomass and productivity of planted and natural stands in relation to climate zone, latitude, elevation, age and species diversity (richness).

Location Six forest climate/vegetation zones in China.

Methods We used a database completed in 2007 and then updated in 2013 that contained extensive records of forest stands (10 m × 10 m plots) across China. The database records included a total of 6153 forest stands (1716 planted forests aged 0–80 years and 4437 natural forests of aged 0–400 years), located from 18.1 to 53.2° N and 75.53 to 131.8° E, and between elevations of 7 and 4240 m above sea level. These forests were grouped into six climate zones for comparisons.

Results Under generally similar physical conditions (climate zones) to those in natural forests and despite having low diversity (i.e. often a single tree species), plantations aged 0–80 years already had similar biomass but much higher productivity, and thus much higher carbon sequestration rates, than natural forests. Tree biomass, productivity and their above/below ground ratios showed stronger latitudinal and elevational trends in natural forests than in planted forests. No difference in productivity was observed between the planted forests with one or two species; in natural forests, however, high diversity usually led to high productivity.

Main conclusions The differences in performance between planted and natural forests were mainly explained by: (1) age (the plantations were in early succession), (2) elevation (plantations were located at lower elevations), and (3) species selection (only highly productive species were planted). As the plantations were all still young, closer monitoring of their performance is needed.

Keywords
Carbon sequestration, China, comparison, elevation, functions, latitude, plantations, restoration, species selection, succession.

INTRODUCTION

Ecologists generally accept that biodiversity can enhance productivity, stability and other ecosystem functions (Loreau *et al.*, 2002). In addition to being affected by biodiversity, ecosystem characteristics may also be greatly affected by species composition (or identity) related to traits (e.g. Huston, 1997) and evenness (Polley *et al.*, 2003; Zhang *et al.*, 2012). New studies, on the other hand, show that the relative importance of these factors might also depend on ecosystem type and successional stage (Laughlin & Moore, 2009; Doherty *et al.*, 2011). Various other factors such as geographical context (e.g. setting) and associated physical/ecological conditions may also play highly variable but significant roles (e.g. Grace *et al.*, 2007; Ma *et al.*, 2010).

Over the past few decades, ecosystem functioning has mostly been studied using experiments in grasslands/greenhouses

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(plants) or microcosms in which species number, population density and abiotic factors are controlled (Hooper *et al.*, 2005). In other words, in almost all such experiments the purpose is to identify the effect of biodiversity (richness and evenness) on productivity and the contribution of physical factors is not the focus. Observations and inferences from natural settings have also occasionally been reported (Griffin *et al.*, 2009; Jiang *et al.*, 2009; Paquette & Messier, 2011; Zhang *et al.*, 2012; Ruiz-Benito *et al.*, 2014). Positioned between these two 'extreme' cases of highly controlled and uncontrolled systems are forest plantations. World-wide restoration efforts have resulted in the establishment of many forest plantations in which some variables (e.g. species, density) are at least partially controlled and others are not. While natural forests have been studied extensively with regard to aspects other than those directly linked to diversity–function relationships, these plantations have perhaps been underappreciated as research sites for determining how biodiversity and other factors influence ecosystem functions.

Forest plantations differ from plantings in standard biodiversity experiments or in natural systems in several ways (Scherer-Lorenzen *et al.*, 2005). For example, plantations in which only species and density are initially manipulated are intermediate in terms of controlled (experiments) and uncontrolled (natural forests) variables. Habitat heterogeneity is seldom a factor in standard biodiversity experiments but is a factor in forest plantations, although to a lesser degree than in natural settings because plantations are often located in defined landscape units (e.g. in an old field, a clear cutting, or burned area) within which environmental conditions are relatively homogeneous. Also, unlike grassland or microcosm biodiversity experiments, in which the range in species number is typically large (e.g. 1–16 or 1–32 species; Hooper *et al.*, 2005; Spehn *et al.*, 2005) and species are randomly chosen from a species pool, forest plantations use very few species (often only one) at one time (Lugo, 1992) and the species are usually carefully chosen to be fit for high productivity. Forest plantations also differ from natural forests with natural successional processes, in that the history of species assemblage is determined at least initially by forest managers (Fig. 1; Ren *et al.*, 2012). Because of these features, plantations offer some unique opportunities for us to simultaneously address the roles of biotic (i.e. richness, species identity/composition, density, age) and abiotic factors (e.g. latitude, elevation and climate) in biomass and productivity that either well-controlled experiments or natural forests could not.

As a consequence of ongoing afforestation efforts, China now has more forest plantations than any other country, constituting *c.* 25% of the world-wide plantation area (del Lungo *et al.*, 2006). The land area with forest plantations in China has increased from 4.5% in 1964 to 33.8% in 2003 (Fang *et al.*, 1996; Guo *et al.*, 2013). Hui *et al.* (2012) investigated biomass–productivity relationships using the database developed in China in which data from natural and planted forests are pooled. Here, using the extensive data from plantations in China, we compare the following properties of plantations and natural forests: leaf area index (LAI), density, biomass and productivity of tree species. We then investigate how these properties are related to age (succession), tree richness versus species identity, and other possible factors such as climate, latitude and elevation. Finally, we consider the implications of our results for future restoration efforts. We hypothesize that planted forests will exhibit fundamental differences in community property and performance from natural forests, mainly due to human selection of site, species and planting density. We believe that comparing the two types of forests, especially those of the same age, could offer new insights regarding forest performance such as productivity and carbon sequestration rate (especially for plantations; Lugo, 1992).

Figure 1 Examples of a pair of planted and natural forest located in the same climate zone in China. Top: an *Acacia mangium* plantation aged 16 years in central Guangdong, Heshan City (112°53′12″ E, 22°40′10″ N). Bottom: a subtropical monsoon evergreen broadleaved forest aged *c.* 400 years also in central Guangdong, Zhaoqing City (112°30′40″ E, 23°09′21″ N) dominated by *Castanopsis chinensis*, *Schima superba* and *Cryptocarya chinensis*.

METHODS

We used a database that contained extensive records of both natural and planted forest stands (10 m × 10 m plots, following the technical National Forest Resource Inventory standards established by the Chinese Ministry of Forestry) across China (Fig. S1 in Supporting Information). The database was based on direct field measurements, publications (Tang *et al.*, 1999; Hui *et al.*, 2012) and systematic inventory reports of tree biomass and productivity (e.g. Chinese Ministry of Forestry, 1999) that were constantly updated before the analyses in this study. The database records include 6153 forest stands (1716 for planted forests aged 18.94 ± 10.62 years and 4437 for natural forests aged 64.51 ± 50.54 years), located from 18.1 to 53.2° N and 75.53 to 131.8° E, and between elevations of 7 and 4240 m above sea level. The forests were grouped into six of a total of eight climate–vegetation zones classified by Wu (1980), who jointly considered climate, potential vegetation distribution and latitudinal, longitudinal and vertical zonality (Table S1). Two of the eight zones did not include enough planted forests for comparison with natural forests and thus were excluded from our analyses. Additional physical factors included site identity and location (latitude, longitude, elevation), and biotic variables included tree age, height, diameter at breast height (d.b.h.), density, LAI and above- (shoot) and belowground (root) biomass and productivity, as well as the biomass and productivity of leaves, stems and branches (Feng *et al.*, 1999; Ni *et al.*, 2001).

The individuals with d.b.h. ≥ 2 cm were treated as overstorey trees and those with a height < 1.5 m were classified as the understorey layer, which also included shrubs and herbaceous species. We used the 'standard tree' method (Ni *et al.*, 2001; Hui *et al.*, 2012), which is most commonly used for biomass and productivity measurements. About 10 and 20 plots were established for sampling within each planted and natural forest stand, respectively, although the number of plots sometimes varied depending on the area of the forests. On each plot, five to seven standard trees of each species within a plot (if available) were selected for cutting and weighing of the component parts such as stem, roots, branches and leaves. The selection of a tree was based on the height and d.b.h. as measured above; that is, for three individuals with average mean sizes, one or two individuals were selected as smaller trees and two as bigger trees, respectively. The biomass for the entire plot was then estimated based on the mean biomass of each tree obtained from the standard tree data and the total number of trees found on the plot. The coarse roots of the tree were dry weighed and the fine roots were estimated. Total LAI of a forest stand was calculated by: LAI = (projected leaf area/leaf weight) × total leaf biomass. Additional details regarding biomass and LAI measurements are provided by Ni *et al.* (2001).

Biomass was measured directly by harvesting and weighing above- and belowground vegetation where feasible or was estimated by using regression equations based on field measurements of tree density, d.b.h. and/or height. The total biomass of each tree was the sum of both above- and belowground biomass which included the total weight of all above- and belowground parts. Net primary productivity (NPP) was estimated based on annual increments of total biomass (leaf, stem, branch and root) obtained by multiplication of the proportion of tree biomass represented by the tissues and their growth rate in the most recent 3–5 years based on an assumption of allocation among different tissue types for different species and in different regions (Ni *et al.*, 2001).

Unlike the planted forests for which there are very few different species in each stand (only one or two species in most cases) – and which are therefore accurately recorded – researchers usually measure dominant tree species in natural forests, and thus the tree species lists are often not complete. This was especially the case for subtropical evergreen and tropical rain forests. In this study, our analyses only included the richness data that could be confirmed based on the detailed sampling description in the original literature. For more detailed and complete information about the methodology used in developing the database see Luo (1996), Tang *et al.* (1999) and Ni *et al.* (2001). Additional and updated information on the database is provided by Hui *et al.* (2012).

Natural forests were broadly and loosely defined to include all major forest types that can regenerate themselves. The plantations were mostly in the early to middle stages of succession and grew under natural conditions after initial planting, i.e. no additional fertilizer or water was applied. We did not include diversity, biomass or productivity of the understorey vegetation in our calculations due to limited information. Comparisons of natural forests and plantations can provide insight into the factors affecting the diversity–ecosystem functioning relationship and other aspects such as biomass carbon sinks, but such comparisons are only meaningful if they are based on long-term evaluation of performance (ideally through the whole successional cycle) (Doherty *et al.*, 2011). Because almost all planted forests are still in early succession (0–80 years old), in addition to comparing all planted and natural forests (up to 400 years old) in our records, we also compared the two types of forests with the database restricted to forests that were 0 to 80 years old; the number of planted forests in the restricted database remained at 1716 but the number of natural forests was reduced to 3359.

We used *t*-tests, *F*-tests and analyses of variance (ANOVAs) for general comparisons of several properties of planted and natural forests. We used regression analysis to examine the relationships between LAI, tree diversity, tree density, tree biomass and tree productivity and also to examine the relationships between above- and belowground biomass and between above- and belowground productivity. In the regression analyses, the original data were log-transformed before analysis to meet the specific requirements such as normality or the assumptions of homogeneity or to be consistent with similar analytical procedures in previous studies. To comparatively examine the effects of selected biotic and abiotic variables on productivity in both types of forests, we conducted multivariate regression analyses. Since some of the variables could be closely interrelated and confounded, to reduce the covariation or data redundancy we performed principal component analysis (PCA) for data deduction before multivariate analyses using SAS (SAS Institute, 1999).

RESULTS

General comparison across stands, latitudes and altitudes

On average, the planted forests were located at significantly lower elevations (609 ± 563 m vs. 1615 ± 1134 m; $t = 65.14$, $P < 0.0001$) and latitude (31.54 ± 7.41 vs. 32.95 ± 7.43; $t = 5.96$,

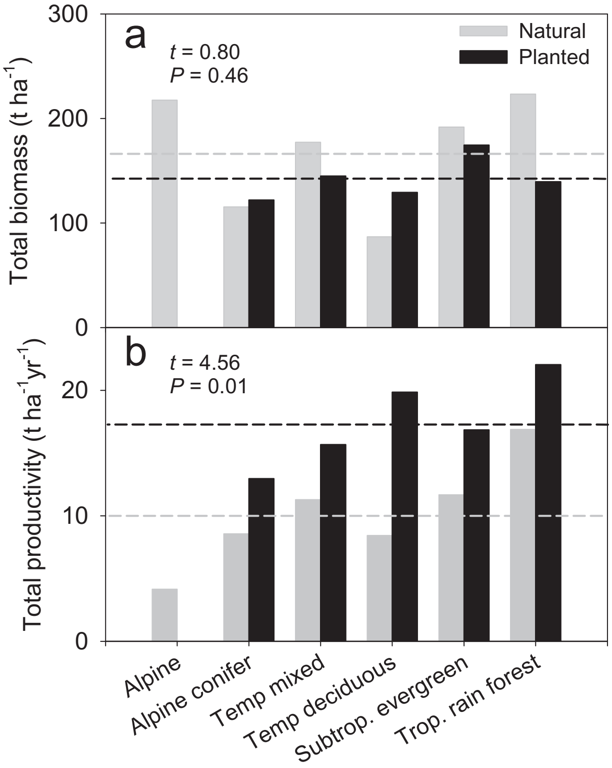

Figure 2 Comparisons of biomass (a) and productivity (b) between planted and natural forests across climate zones in China. Data from forests of all ages are included. The 'alpine' forest group was excluded from the *t*-tests because no plantations have been established in that zone. The dashed lines represent the mean values for natural (grey) and planted forests (black).

$P < 0.0001$) than natural forests within the same climate zones. The highest mean biomass was in the natural tropical rain/seasonal rain forest (223 t ha^{-1}) followed by Qinghai-Tibet Plateau (218 t ha^{-1}), and the lowest mean biomass was in the natural warm temperate deciduous forest (86.8 t ha^{-1}). Across the climate zones, natural forests had slightly higher biomass (169 ± 56 t ha^{-1}) than planted forests (142 ± 20 t ha^{-1}) but the difference was not significant (paired *t*-test, $t = 0.80$, $P = 0.46$; Fig. 2a). However, natural forests exhibited greater spatial variation in biomass than planted forests across forest stands ($F = 0.7$, $P < 0.0001$).

Despite low diversity (often a single tree species), planted forests had similar biomass (Fig. 2a) but much higher productivity than natural forests when data from all forests were used regardless of age (17.5 ± 3.6 vs. 10.2 ± 4.3 t ha^{-1} year^{-1}; paired *t*-test, $t = 4.56$, $P = 0.01$). Among natural forests, productivity was highest in the tropical seasonal rain forest (16.9 t ha^{-1} year^{-1}) and lowest in the alpine forest (4.2 t ha^{-1} year^{-1}). Among planted forest, the tropical seasonal rain forest had the highest productivity (22.1 t ha^{-1} year^{-1}) while the cold temperate conifer forest had the lowest (13.0 t ha^{-1} year^{-1}; Fig. 2b). Again, across forest stands, natural forests showed larger spatial variation in productivity than planted forests ($F = 1.83$, $P < 0.0001$). Latitudinal trends in biomass and productivity were not evident for planted forests but were evident for natural forests (Fig. 3a,b). Similar results were obtained when the analyses were restricted to data for forests that were 0–80 years old or when biomass (or height, d.b.h.) was controlled (data not shown).

When all data were combined for both kinds and all ages of forests, both biomass and productivity declined with latitude ($r = 0.09$, $F = 35.46$, $P < 0.0001$ for biomass; $r = 0.17$, $F = 114.13$, $P < 0.0001$ for productivity). The above/belowground biomass ratio declined with latitude in both planted and natural forests (Fig. 3c). However, the above/belowground productivity ratio declined significantly with latitude in natural forests (Fig. 3d). Similar results were obtained when the analyses were restricted to data for forests that were 0–80 years old.

There were also significant differences in the properties of natural versus planted forests as related to elevation. When stand data from all ages were combined, total biomass increased with elevation in natural forests but not in planted forests (Fig. 4a). The total productivity increased with elevation in natural forests but decreased with elevation in planted forests (Fig. 4b). The above/belowground biomass ratio and above/belowground productivity ratio were not significantly related to elevation in natural forests but increased with elevation in planted forests (Fig. 4c,d). As before, similar results were obtained when the analyses were restricted to data for forests aged 0–80 years (data not shown).

Age-dependent productivity and biomass

Productivity usually peaks within 5–30 years in planted forests but after a much longer time (20–60 years on average) in natural forests (Fig. 5). For forests from 0 to 80 years old, tree LAI, total tree productivity (shoot + root) and total tree biomass (shoot + root) were higher in plantations than in natural forests ($t = 9.83$, d.f. = 4529, $P < 0.0001$ for LAI; $t = 23.87$, d.f. = 4808, $P < 0.0001$ for total productivity; and $t = 8.28$, d.f. = 5020, $P < 0.0001$ for total biomass) (Fig. 5).

For forests aged 0 to 80 years the shoot/root biomass ratio, shoot biomass and root biomass were significantly higher in planted forests than in natural forests ($t = 11.2$ and $P < 0.0001$ for shoot/root biomass ratio; $t = 9.39$ and $P < 0.0001$ for shoot biomass; and $t = 3.8$ and $P = 0.0001$ for root biomass) (Fig. S2). The shoot/root biomass ratio was the highest in subtropical evergreen forests (4.38) and lowest in cold temperate conifer forests (2.42). Planted forests also had higher shoot productivity ($t = 21.54$, $P < 0.0001$) and root productivity ($t = 22.83$, $P < 0.0001$) than natural forests, but the shoot/root productivity ratio did not differ between the two types of forests (8.46 vs. 7.57; $t = 1.0$, $P = 0.32$) (Fig. S2).

In comparisons between younger (0–80 years) and older (81–400 years) natural forests, older forests had higher shoot/root biomass ratios ($t = 3.17$, $P = 0.0002$), shoot biomasses ($t = 12.8$, $P = 0.0001$) and root biomasses ($t = 21.8$, $P < 0.0001$). Older forests also had higher shoot/root productivity ratios ($t = 7.3$, $P < 0.0001$) and root productivity ($t = 3.72$, $P = 0.0002$), but the two age groups of natural forests did not significantly differ in shoot productivity ($t = 0.52$, $P = 0.61$) (Fig. S2).

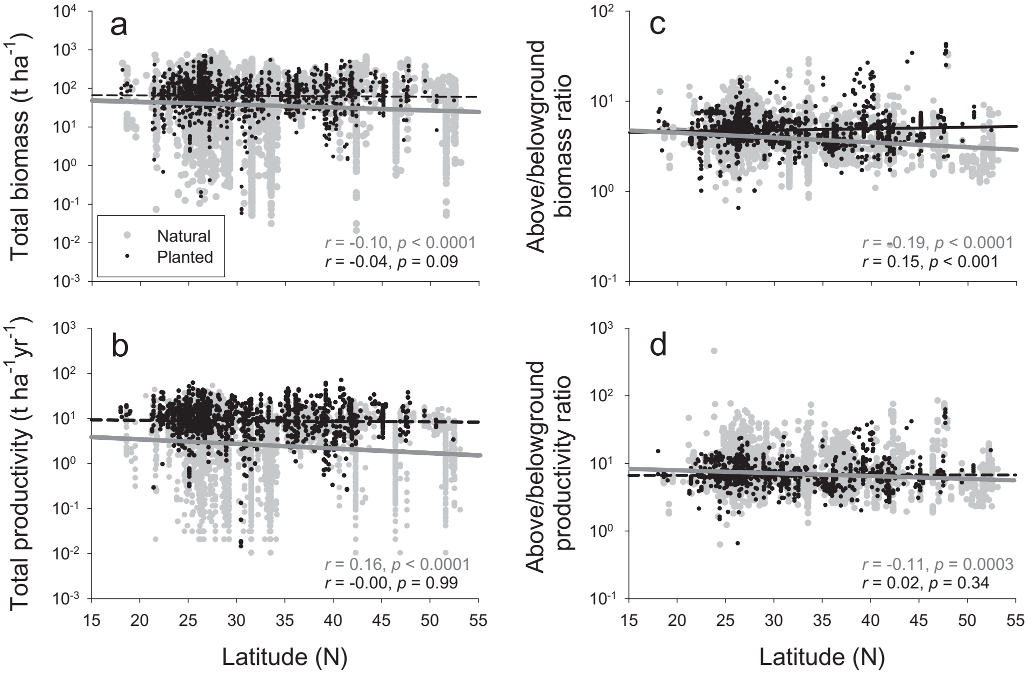

Figure 3 Relationships between latitude and (a) total biomass, (b) productivity, (c) above/belowground biomass ratio, and (d) above/belowground productivity ratio of natural and planted forests in China. Data from forests of all ages are included.

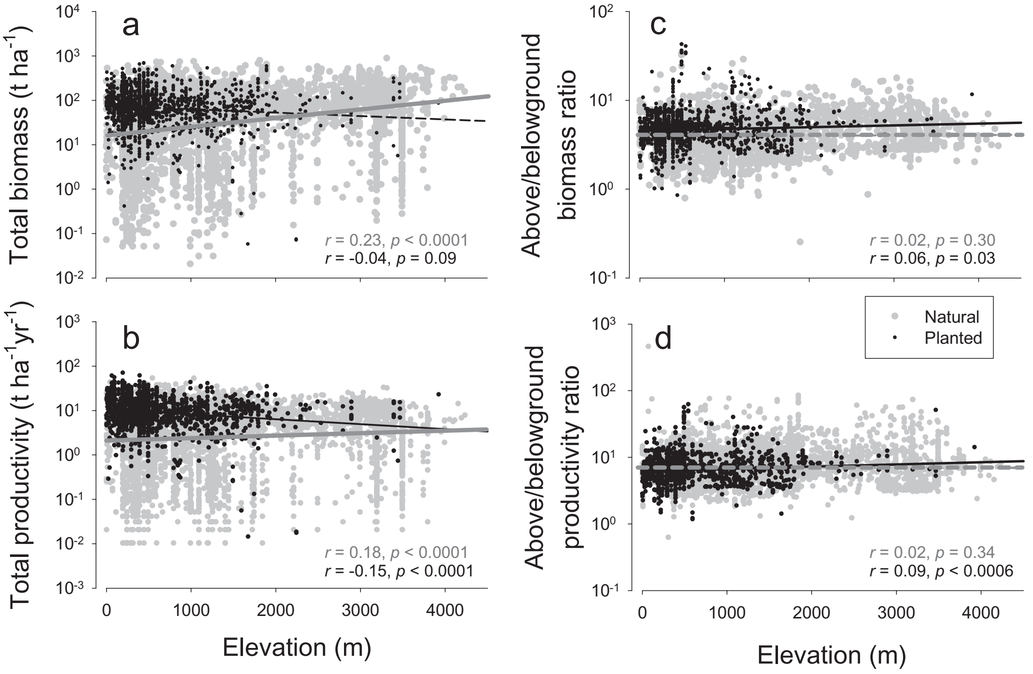

Figure 4 Relationships between elevation and (a) total biomass, (b) productivity, (c) above/belowground biomass ratio, and (d) above/belowground productivity ratio of natural and planted forests in China. Data from forests of all ages are included.

Relationships among diversity, density, biomass, LAI and productivity

Strong positive relationships between shoot and root biomass and between shoot and root productivity were evident in both planted and natural forests based on data from forests of all ages (i.e. allocation was isometric; $P < 0.0001$ for all four regressions in Fig. S3). Results were similar when data were restricted to forests that were aged 0 to 80 years (data not shown). Regression slopes did not significantly differ between

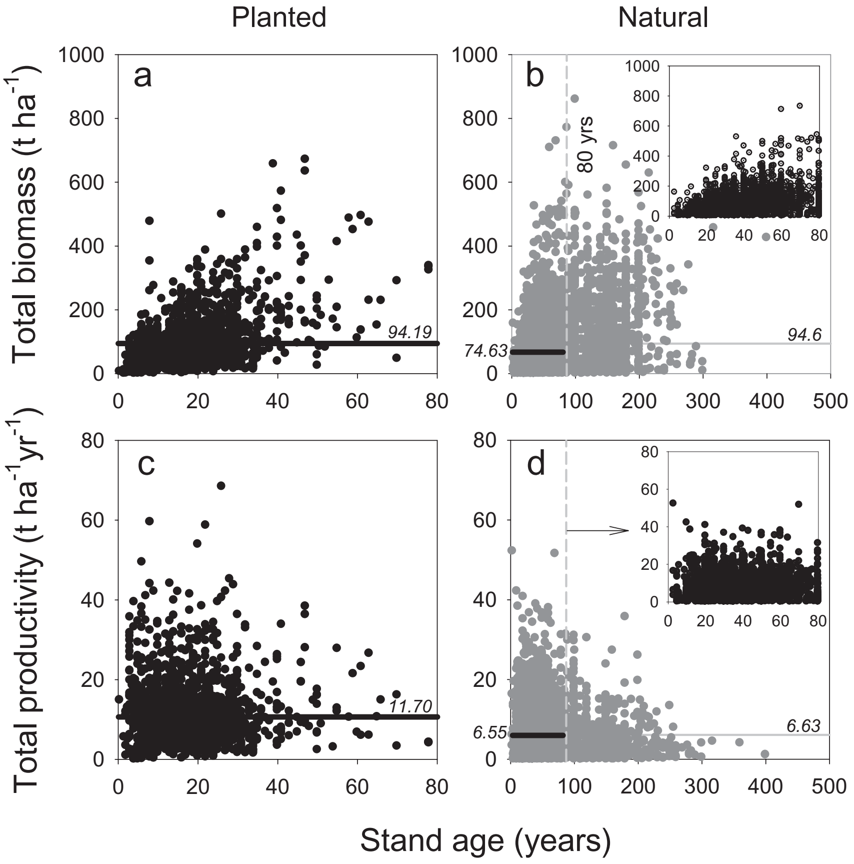

Figure 5 Total biomass (above- and belowground) of (a) planted and (b) natural forests, and total productivity (above- and belowground) of (c) planted and (d) natural forests (see also Fig. 2). The grey, dashed vertical lines in (b) and (d) indicate natural forests up to 80 years old for comparison with planted forests of the same age. The black horizontal lines in all panels indicate the means for forest from 0 to 80 years old. The thin, grey horizontal lines in (b) and (d) indicate the means for natural forests of all ages. Inserted panels are the enlarged diagrams for natural forests aged 0–80 years. For forests from 0 to 80 years old, tree leaf area index (LAI), total tree productivity (shoot + root) and total tree biomass (shoot + root) were higher in plantations than in natural forests ($t = 9.83$, d.f. = 4529, $P < 0.0001$ for LAI; $t = 23.87$, d.f. = 4808, $P < 0.0001$ for total productivity; and $t = 8.28$, d.f. = 5020, $P < 0.0001$ for total biomass).

the two types of forests and between the two forest age groups ($P > 0.05$).

Productivity did not significantly differ between the planted forests with one versus two tree species ($F = 1.06$, $P = 0.40$) (Fig. 6a). In natural forest, however, productivity was positively related to diversity (tree species richness) (Fig. 6b). For both planted and natural forests of all ages, productivity was positively related to LAI (Fig. 6c) and biomass (Fig. 6e). Productivity was positively related to tree density in natural forests but not in planted forests (Fig. 6d). Similar results were obtained when the analyses were restricted to data for forests that were aged 0–80 years (data not shown).

Planted and natural forests exhibited similar hump-shaped or unimodal relationships between tree density and biomass ($r^2 = 0.02$, $F = 13.74$ and $P < 0.0001$ for planted forests; $r^2 = 0.02$, $F = 54.4$, and $P < 0.0001$ for natural forests) (Fig. S4). In other words, biomass increased with tree density when density was low but decreased when density was too high.

Overall, when all selected variables were considered together, PCA indicated that some variables overlapped in the bivariate plot (Fig. S5). To confirm the presence of collinearity, we performed 'collinearity diagnostics' using the SAS Proc reg procedure (SAS Institute, 1999) and found that tree height, d.b.h. and LAI had a variance inflation factor (VIF) of 19.90, 28.28 and 93.80, respectively (the remaining variables had VIFs of 0.99–2.25). Tree height and d.b.h. were strongly correlated with stand age and LAI with tree biomass ($r > 0.95$). Following Belsey *et al.* (1980) which stated that VIF > 10 would indicate the presence of collinearity (see also Graham, 2003), we removed these three redundant variables in further multivariate analyses.

Multiple regressions showed that more selected variables exhibited a significant influence on productivity in natural (eight out of nine) than in planted forests (four out of nine; Table 1). Interestingly, longitude and mean annual temperature and precipitation had significant effects on the productivity of natural forests but not on that of planted forests (Table 1). While most results from multivariate analyses confirmed those obtained from bivariate analysis, there were a few exceptions. For example, multivariate analysis showed that altitude had no significant effect on productivity in natural forests, but bivariate regression showed otherwise (Fig. 4). Bivariate analysis showed that density was positively related to productivity only in natural forests but multivariate analysis showed that such positive relationship existed in both natural and planted forests (Fig. 6d).

DISCUSSION

Plantations, which account for 7% of the world's forest cover but could potentially provide 50% or more of the global industrial roundwood demand (del Lungo *et al.*, 2006), represent planted ecosystems that can be useful for investigating ecological theories. Plantations are gaining increased attention from ecologists and the public, not only because of their economic value but also because of their ecological and functioning roles in

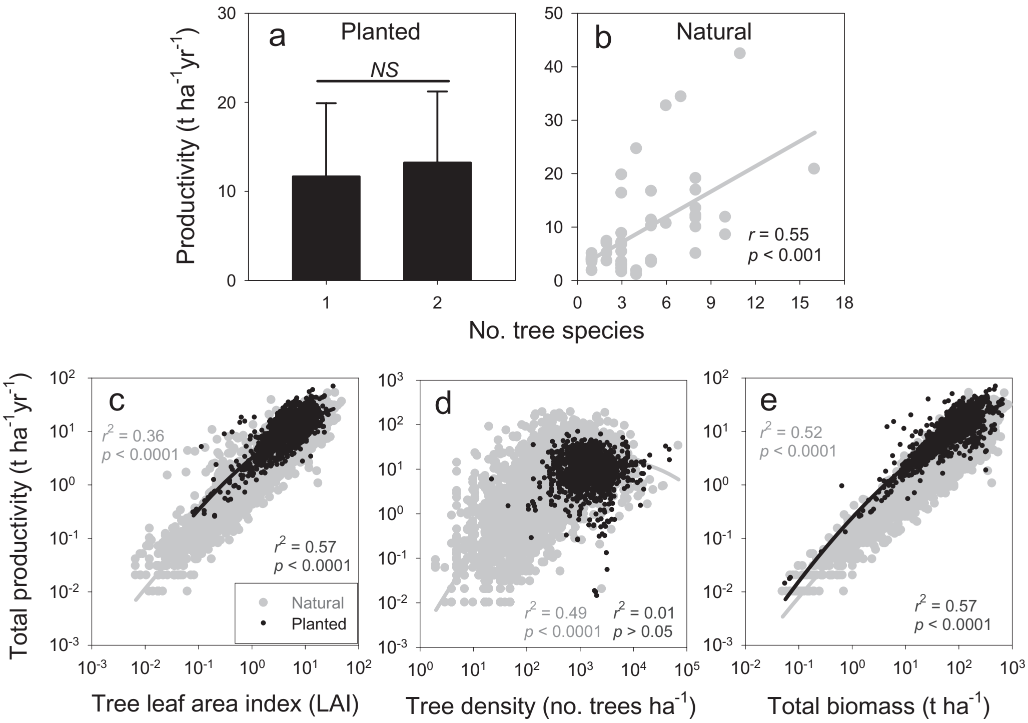

Figure 6 Top: relationships between diversity (number of tree species) and productivity in planted (a) and natural forests (b) in China. Data from forests of all ages are included. Bottom: relationships of productivity with leaf area index (LAI) (c), tree density (d), and tree biomass (e) in planted and natural forests in China. Note that tree density has a much narrower range in planted forests than in natural forests because of planting design. Data from forests of all ages are included, but data from forests aged 0 to 80 years old generated similar patterns (data not shown).

Table 1 Results of multiple regression analysis between productivity and selected variables in planted versus natural forests in China after principal components analysis data deduction (see Fig. S5).

		Planted			Natural		
Source	d.f.	Type III SS	*F*	*P*	Type III SS	*F*	*P*
Latitude (°N)	1	5.5	0.2	0.64	42.8	6.0	**0.01**
Longitude (°E)	1	56.4	2.2	0.14	153.1	21.6	**< 0.0001**
Altitude (m)	1	559.7	22.0	**< 0.0001**	21.2	3.0	0.08
Tree species richness	1	89.7	3.5	0.06	20.5	2.9	**0.004**
Mean annual temperature (°C)	1	27.4	1.1	0.30	73.2	10.3	**0.001**
Mean annual precipitation (mm)	1	68.7	2.7	0.10	76.6	10.8	**0.001**
Age (years)	1	1 061.7	41.7	**< 0.0001**	4 099.0	578.0	**< 0.0001**
Density (no. trees ha^{-1})	1	135.2	5.3	**0.02**	1 854.8	261.5	**< 0.0001**
Total biomass (t ha^{-1})	1	29 258.1	1149.5	**< 0.0001**	30 818.0	4345.5	**< 0.0001**

SS, Sums of Squares.
Bold-faced values indicate significant effects.

world ecosystems. They offer a novel alternative to typical and traditional experimental approaches used in grasslands and greenhouses. Unlike natural forests, in which species join the community naturally and no factor is controlled, species and tree densities in planted forests are usually carefully selected but without further manipulation such as fertilization, addition of water or artificial thinning. Our study demonstrates that there is much to learn from the forest plantations where species number, identity, composition and abundance are controlled, while some degree of heterogeneity is maintained or uncontrolled (Lugo, 1992, 1997).

One of the most striking results in our study is that plantations had much higher productivity than natural forests across all climate zones, while biomass was similar (Fig. 2). We discuss in detail several possible underlying mechanisms for this pattern in the following subsections. The positive relationship between tree density and productivity in natural forests but not in planted forests could be due to the fact that planted forests: (1) have only a few species (often one or two are initially planted); (2) have only a narrow range of tree density as a result of the original planting design (Fig. 6d); and (3) are still in early succession.

The similar and strong positive allometric (isometric) correlations between shoot and root biomass and between shoot and root productivity in both planted and natural forests with vastly different species in China (Fig. S3) might be expected (Enquist & Niklas, 2002; Yang *et al.*, 2009). In addition, when based on log-transformed data, these relationships showed little dependence on age (Yang & Luo, 2011). Related studies such as Coyle *et al.* (2008) also found strong and isometric correlations between above- and belowground biomass in stands of loblolly pine. While such correlations are expected, recent studies also suggest close links between above- and belowground biodiversity, not only for plants but also for animals and microbes (Hooper *et al.*, 2005; Bardgett & Wardle, 2010). This is partly because both biomass and productivity are related to diversity and partly because above- and belowground elements are simultaneously affected by the same physical factors and disturbances.

Latitudinal and elevational trends

When data were combined for forests of all ages (0–80 years for planted forests and 0–400 years for natural forests), planted forests did not show any latitudinal trend in biomass and productivity whereas natural forests did. The results from multivariate regression that neither annual temperature nor precipitation affected productivity in planted forests also confirm this because these two climate variables are often inversely related to latitude (Fig. S5). Much of the variation (as indicated by residuals) in planted forests could be due to elevational differences among sites and to the effect of species selection. The causes for the decline in the ratios of above/belowground biomass and above/belowground productivity with latitude (with one exception: the above/belowground productivity ratio in planted forests) remain elusive. However, as was the case with the relationships between latitude and biomass or productivity, most of the variations in these ratios among stands of both planted and natural forests could be due to difference in elevation. The relationships of latitude with biomass, productivity, above/belowground biomass ratio and above/belowground productivity ratio were evidently unaffected by stand age, i.e. the relationships were similar whether the analysis included data from all stands (0–400 years old) or only from those that were 0–80 years old.

Unlike the latitudinal patterns, the difference in elevational patterns between planted and natural forest could mostly be due to the fact that the planted forests are located at significantly lower elevations than natural forests. The difference in responses of the two types of forest to elevation change could not be explained by forest age alone. Whether the difference is due to the selection of species in planted but not in natural forests is unclear. In addition, the significant effect of longitude on productivity in natural but not planted forests requires further exploration (Table 1).

Age-dependent performance

The history of a community assembly clearly plays an important role in shaping the diversity–productivity and other relationships (e.g. Pan *et al.*, 2004; Ren *et al.*, 2010; Wang *et al.*, 2011). The major difference in productivity (not biomass per se) between natural and planted forests highlights the importance of age (Figs 5 & S2). Most of the plantations are still in early successional stages (as reflected by their higher shoot/root biomass ratio; Fig. S2). The biomass in the plantations could continue to increase as the planted forests mature, but productivity could decline drastically (e.g. Luo *et al.*, 2002; Guo, 2003).

That the productivity of plantations within each climate zone was twice that of natural forests indicates that plantations have a high potential for carbon sequestration in the future. As indicated above, this is at least partly because plantations (1) were still in early stages of succession, and (2) used highly productive tree species. This is evident by comparing the natural and planted forests of roughly the same age (Figs 5 & S2). Moreover, planted forests are at lower elevation and latitude and presumably have longer growing seasons over which to accumulate biomass. Although for both planted and natural forests elevation is inversely related to latitude (not significant) the relationship is better described as unimodal, especially for natural forests (Fig. S6). This could underlie observed differences between planted and natural stands.

The age factor is complicated by the life span of dominant species, especially in planted forests. Tree species with short life spans mature more quickly than those with longer life spans. Thus, when forests with different dominant species are pooled, some underlying relationships that are partly controlled by age may be masked. The comparison between younger forests (0–80 years old) and older forests (81–400 years old) in Figs 5 & S2 suggests that, the young forests of both types hold great potential to grow and thus to fix and store large amounts of carbon in the future (Guo *et al.*, 2013).

Plantations with even-aged individuals are ideal for examining many allometric relationships (Deng *et al.*, 2012). In warmer regions, the difference in biomass between planted and natural forests was smaller than in colder regions. If age is important, the difference could be at least partly due to the faster growth of planted species in cold regions. In other words, planted species require less time than native species in natural forests to reach their maximum size in cold regions.

Diversity, species identity and productivity

Despite the broadly observed diversity effects, selecting a few ‘right’ species when the planting of many species is not feasible could achieve high productivity. Huston (1997) discussed the importance of species identity (see also Symstad *et al.*, 1998) which is related to life history and thus growth rate. Our study shows that, in the same climate zones, natural forests with high diversity did not have higher biomass than plantations with low diversity. Plantations have higher biomass than natural forests because plantation managers tend to choose the most productive species for the specific region. For plantations, species identity and planting density greatly affect biomass and productivity (Guo, 2011).

It was not surprising that productivity was not significantly higher in plantations with two tree species than in those with only one species (Fig. 6a). Even in well-controlled seeding experiments, the productivity of plots with only one to three species is usually highly variable and unaffected by species number (e.g. Hooper *et al*., 2005; Spehn *et al*., 2005). Therefore, plantations are good examples of the sampling/trait effects reflected in some grassland experiments. The positive diversity–productivity relationship in natural forests, however, might be at least partly responsible for the reduced productivity along latitudinal gradients over which tree richness usually declines (Rosenzweig, 1995).

An important limitation of the current study is that the contributions of the understorey to biomass, productivity and ecosystem services were not considered. Although the focus of forestry is on the production of timber, the ecosystem services provided by the forest reflect the contributions of all species, not only the trees (Lugo, 1997). Thus, knowing the contribution from both above- and understory species would help draw a more complete picture for understanding forest functioning and overall performance.

Implications for future plantation and restoration

Our comparative study between natural and planted forests based on long-term data has yielded new insights into the structural or functional relationships among selected variables. Collectively, these results highlight the differences between planted and natural forests especially when some of the relationships are clearly age dependent. The results suggest that short-term patterns must be interpreted with caution as the long-term trends still remain to be seen, especially with the high possibility that the productivity of planted forests may decline over time. Any one-time snapshot of the diversity–function relationship should be considered in the context of the full successional cycles. The observed peaks of productivity within 5–30 years (20 on average) in planted forests versus 20–60 years (40 on average) in natural forests (Fig. 5) offer some guidelines regarding plantation rotation (i.e. from planting to harvesting).

Given the increasing restoration efforts and pressure from humans and climate change, plantations and other forms of restored ecosystems around the world will play even greater role in carbon sequestration and storage, ecosystem resilience and ecosystem functioning or services (e.g. timber, ecotourism, water quality; Sedjo & Botkin, 1997; Ren *et al*., 2012). It is critical to continue monitoring multiple community variables simultaneously in both types of forest including diversity, density, spatial distribution and the temporal sequence of continuously colonizing species (Guo *et al*., 2004; Paquette & Messier, 2011). Future plantations should also shift strategy (e.g. in species selection) as needed by taking climate change, the introduction of non-native species and changes in surrounding habitats into account (Liu *et al*., 1993). Ultimately, in addition to many other socioeconomic purposes and services, a long-term goal for the massive plantations world-wide is to make them into suitable habitats for many native species (Lugo *et al*., 1993).

In short, our analysis of an extensive database indicates that productivity and biomass are generally higher in planted forests than in natural forests in China. These differences probably result from differences in stand age and from the planting of highly productive species in plantations. This study has several important limitations. First, the plantations were still young, and it is likely that productivity will decline as the trees age. Second, the study did not include some important biodiversity effects, including those on nutrient cycling and stability. Third, the study was limited to trees without considering understorey plants, animals and microorganisms or diseases (Lugo, 1997). These limitations should be addressed in future research.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Figure S1 Distribution of forest types and sampling plots across China.

Figure S2 Shoot/root ratios of planted and natural forests.

Figure S3 Allometric relationships in planted and natural forests in China.

Figure S4 Relationship between biomass and tree density.

Figure S5 Results from principal component analysis (PCA).

Figure S6 Relationship between latitude and elevation of forests in China.

Figure S7 Relationships between tree size (height) and productivity.

Table S1 Climate/vegetation zones in China.

Appendix S1 Additional references on biomass and productivity measurements.

Appendix S2 Data used in this study (with updates).

BIOSKETCHES

Qinfeng Guo has broad interests in community ecology and biogeography. He is currently working on biodiversity patterns at various scales that may affect the process and patterns of biotic invasions and ecosystem functions. He also studies how life-history traits and genetics may influence species invasiveness and how history and habitat characteristics may affect invasibility.

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