RESEARCH PAPER

Above-ground forest biomass is not consistently related to wood density in tropical forests

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ABSTRACT

Aim It is increasingly accepted that the mean wood density of trees within a forest is tightly coupled to above-ground forest biomass. It is unknown, however, if a positive relationship between forest biomass and mean community wood density is a general phenomenon across forests. Understanding spatial variation in biomass as a function of wood density both within and among forests is important for predicting changes in stored carbon in response to global change, and here we evaluated the generality of a positive biomass–wood density relationship within and among six tropical forests.

Location Costa Rica, Panama, Puerto Rico and Ecuador.

Methods Individual stem data, including diameter at breast height and spatial position, for six forest dynamics plots were merged with an extensive wood density database. Individual stem biomass values were calculated from these data using published statistical models. Total above ground biomass, total basal area and mean community wood density were also quantified across a range of subcommunity plot sizes within each forest.

Results Among forests, biomass did not vary with mean community wood density. The relationship between subcommunity biomass and mean wood density within a forest varied from negative to null to positive depending on the size of subcommunities and forest identity. The direction of correlation was determined by the associated total basal area–mean wood density correlation, the slope of which increased strongly with whole forest mean wood density.

Main conclusions There is no general relationship between forest biomass and wood density, and in some forests, stored carbon is highest where wood density is lowest. Our results suggest that declining wood density, due to global change, will result in decreased or increased stored carbon in forests with high or low mean wood density, respectively.

Keywords
Atmosphere–biosphere feedbacks, carbon cycle, carbon storage, forest dynamics plot, fragmentation, functional traits, global change, lianas, nitrogen deposition, tropical forests.

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INTRODUCTION

A central goal of functional ecology is to mechanistically link changes in species-level traits to ecosystem processes (Lavorel & Garnier, 2002) to understand how such linkages ramify to influence global change (Chapin *et al.*, 2000; Eviner & Chapin, 2003). From this perspective, wood density is a key functional trait within forests (Swenson & Enquist, 2007) in that it may

influence woody biomass and ecosystem carbon stocks (Baker *et al.*, 2004; Malhi *et al.*, 2006). Baker *et al.* (2004) reported a positive correlation between mean tree community wood density and above-ground forest biomass and a number of studies have argued that temporal declines in mean community wood density will cause a decline in above-ground forest biomass and thus terrestrial carbon pools (e.g. Phillips & Gentry, 1994; Körner, 2004; Bunker *et al.*, 2005; Laurance *et al.*, 2006; Keeling &

Phillips, 2007). (Note that mean community wood density is the mean wood density across all trees above a minimum size in a given area of forest, and above-ground forest biomass is referred to simply as 'forest biomass' below unless otherwise noted.) For example, increasing levels of nitrogen deposition (Galloway *et al.*, 2004), solar radiation (Wielicki *et al.*, 2002), atmospheric carbon dioxide, forest fragmentation (Laurance, 1998) and/or increasing liana (woody vine) growth (Condon *et al.*, 1992; Würth *et al.*, 1998; Granados & Körner, 2002; Phillips *et al.*, 2004) may result in a decline in the average wood density of trees within a forest (Phillips & Gentry, 1994; Schnitzer *et al.*, 2000; Nemani *et al.*, 2003; Malhi *et al.*, 2004; Phillips *et al.*, 2004; Stephenson & van Mantgem, 2005; Laurance *et al.*, 2006).

If forest biomass is positively correlated with mean community wood density, a decline in mean community wood density will lead to less carbon stored in forests, potentially leading to a positive feedback between climate change and reductions in forest carbon stocks. There is, however, no mechanistic or theoretical basis to justify a consistently positive relationship between forest biomass and mean community wood density. Specifically, individual diameter growth rate is dependent upon individual wood density but the rate of whole-plant biomass accumulation is not (Enquist *et al.*, 1999). Forests differing in mean community wood density should thus not differ in the rate of biomass accumulation (Enquist *et al.*, 1999; Enquist & Niklas, 2001) such that there is no a priori expectation that forest biomass will uniformly increase with mean community wood density. Furthermore, within a forest the correlation between subcommunity forest biomass and mean subcommunity wood density need not be consistent among forests, and is probably determined by the correlation between subcommunity basal area (i.e. trunk cross-sectional area) summed over all trees in a community (total basal area) and mean subcommunity wood density. This can been seen by first noting that $M_{tot} = N\bar{M}$, where M_{tot} is forest biomass, N is the number of individuals in a forest and $\bar{M}$ is mean individual biomass. Following Chave *et al.* (2005), $\bar{M} = \overline{\rho f(D)}$, where ρ is wood density and $f(D)$ is a function relating tree diameter to individual biomass. Substituting provides forest biomass as a function of wood density and diameter: $M_{tot} = N\overline{\rho f(D)}$.

If wood density and diameter do not covary, forest biomass will increase with mean community wood density. However, individual tree diameter declines with individual wood density within Barro Colorado Island (Chave *et al.*, 2004). This negative correlation at the individual level may cause a null or even negative forest biomass–mean community wood density relationship across space within Barro Colorado Island. In contrast, by first assuming that individual basal area does *not* vary with individual wood density and subsequently simulating the loss of trees with low wood density in Barro Colorado Island, Bunker *et al.* (2005) suggested that forest biomass should increase with mean community wood density in Barro Colorado Island. Assuming that basal area does not vary with wood density is an invalid assumption for Barro Colorado Island (Chave *et al.*, 2004), and it is thus unclear how forest biomass actually varies with mean community wood density in Barro Colorado Island. More generally,

it is unknown if forest biomass varies with mean community wood density among forests or if the relationship between subcommunity forest biomass and mean subcommunity wood density *within* a forest is consistent *among* forests. Given these uncertainties, and the importance of the relationship between forest biomass and mean community wood density for future carbon stocks, it is critical to better understand how forest biomass varies with mean community wood density among and within forests.

In this paper we evaluate how forest biomass varies with mean community wood density among and within six tropical forests that differ in forest biomass, mean community wood density, annual precipitation, species richness and density of individual trees. We also relate forest biomass–mean community wood density correlations to correlations between total basal area and mean community wood density within a forest to provide insight into why forests differ in how subcommunity forest biomass is related to mean subcommunity wood density. In doing so, this paper addresses the following questions: (1) What are the functional relationships between mean community wood density and both forest biomass and total basal area among and within forests, and do within-forest relationships differ among forests? (2) Do the directions and/or strengths of the relationships between mean community wood density and forest biomass and total basal area within a forest vary with the size of subcommunities? (3) How do biotic and abiotic factors such as species richness, climate, time since disturbance, and community-level abundance, biomass, mean wood density and maximum individual biomass affect how forest biomass and total basal area vary with mean community wood density within a forest? (4) Within forests, how are forest biomass–mean community wood density correlations related to total basal area–mean community wood density correlations?

METHODS

We used data from six forest dynamics plots: Barro Colorado Island (Panama) (Condit, 1998; Hubbell *et al.*, 1999, 2005), San Emilio (Costa Rica), Sherman (Panama), Cocoli (Panama), Yasuni (Ecuador) (Valencia *et al.*, 2004) and Luquillo (Puerto Rico) (Thompson *et al.*, 2002) (see also Losos & Leigh, 2004). Data for Barro Colorado Island, Sherman and Cocoli were accessed through the Center for Tropical Forest Science website (http://www.ctfs.si.edu/plots/), and all other plot data were provided directly by one or more authors. Luquillo was heavily disturbed by a hurricane in 1989 and to a much lesser extent by another hurricane in 1998, and all four censuses (1990, 1995, 2000, 2005) were analysed so that the relationship between forest biomass and mean wood density could be examined through time. For each forest as a whole and for each subcommunity within each forest we calculated total above-ground biomass, total tree basal area summed across all individuals, mean community wood density weighted by individual biomass (referred to as 'community wood density', see below), total number of individuals, maximum individual biomass and species richness. Community wood density was calculated by summing across the wood density of each inventoried stem multiplied by its fractional contribution to

whole forest or subcommunity biomass. We weighted mean community wood density by individual stem biomass because the wood density of stems contributing the most to forest biomass will have the greatest influence over stored carbon.

In each plot, all individuals above 1 cm diameter at breast height (d.b.h.) (130 cm) were identified and their d.b.h. was measured. For San Emilio the minimum d.b.h. is 3 cm, but this will have little influence over our analyses as very little biomass is contained in individuals below 3 cm d.b.h. These plots range in size from 4–50 ha and include climates ranging from dry to wet tropical forests (Table 1). Within-forest analyses subdivided each forest plot into non-overlapping subcommunities, made to be as close to square as possible, ranging from 0.05–2 ha. To calculate individual biomass we employed diameter-based, forest-type specific equations from Chave *et al.* (2005). We used the moist forest equation for Barro Colorado Island and Yasuni, the dry forest equation for San Emilio and Cocoli, and the wet forest equation for Sherman and Luquillo.

We also incorporated differences in wood density between species in order to improve biomass estimates (Fearnside, 1997; Chave *et al.*, 2003, 2004; Baker *et al.*, 2004). Biomass is directly proportional to wood density in the equations provided by Chave *et al.* (2005). Wood density data for Barro Colorado Island, Yasuni, Sherman and Cocoli were gleaned from the literature and pre-existing databases (Swenson & Enquist, 2007). The wood density data for San Emilio and Luquillo came from field collections by N. G. Swenson following the methodologies of Cornelissen *et al.* (2003) for trees and Swenson & Enquist (2008) for shrubs. For each individual, wood density was taken as the mean species value, or if the species was not represented in our database, wood density was estimated as the genus mean. In cases where the individual was not identified to genus or wood density data were lacking for a given genus, we used the average wood density of the other individuals within an entire forest dynamics plot. Plot-level wood density was used because most variation in wood density exists among genera and there is spatial variation in plot-level wood density (Baker *et al.*, 2004; Malhi *et al.*, 2006; Swenson & Enquist, 2007).

Summing the biomass and basal area of all stems in each subcommunity provided forest biomass and total basal area, respectively, which were evaluated with respect to subcommunity wood density via linear regression. To address our primary research objectives, we evaluated linear regressions between community wood density and both forest biomass and total basal area among forests and across a range of spatial scales within forests. We also related slopes of these regressions to descriptor variables for each forest, including species richness, climate, time since disturbance, and whole plot-level abundance, biomass, and mean wood density (Table 1 provides these data). To elucidate the influence of total abundance and maximum individual biomass within a subcommunity over the relationship between forest biomass and community wood density, we regressed total abundance and maximum individual biomass against community wood density across subcommunities. These analyses were performed for each forest at the spatial scale for which community wood density explained the most variation in forest biomass. Lastly, we plotted the slopes from forest biomass–community wood density regressions against their corresponding total basal area–community wood density regressions.

Reduced major axis regression lines are provided for significant correlations due to measurement error in the independent variable (i.e. wood density). Ordinary least squares regression lines are also provided for comparison as reduced major axis will, at low r^2 values (< 0.15), provide unreliable slope estimates (O'Connor *et al.*, 2007). All regression analyses were conducted in the software package R (http://www.r-project.org/).

RESULTS

Among the six forests studied here, per-area forest biomass did not vary significantly with whole plot-level community wood density ($P = 0.9$). In contrast, forest biomass did vary spatially with community wood density among subcommunities within each forest, but this relationship was not consistent among forests. Within Barro Colorado Island and Cocoli, forest biomass decreased with community wood density, as did total basal area.

Table 1 Description of forest dynamics plots, including approximate area, annual precipitation (AP), forest-type equation used from Chave *et al.* (2005) to calculate above-ground biomass, the total number of species in each plot, fractions of species with wood density data at the species, genus and plot levels, above-ground biomass, whole plot-level biomass-weighted mean wood density (WD), and abundance.

	Barro Colorado Island (Panama)	Cocoli (Panama)	Luquillo (Puerto Rico)	Sherman (Panama)	San Emilio (Costa Rica)	Yasuni (Ecuador)
Area (ha)	50	4	16	6	12	25
AP (mm)	2600	1950	3500	2850	1600	3100
Equation	Moist	Dry	Wet	Wet	Dry	Moist
Species richness	320	176	152	237	135	1104
Species fraction	0.48	0.5	1	0.42	1	0.27
Genus fraction	0.42	0.4	0	0.44	0	0.6
Plot fraction	0.1	0.1	0	0.14	0	0.13
Biomass (Mg ha^{-1})	301	155	249	205	138	280
WD (kg m^{-3})	545	494	604	595	614	588
Individuals (ha^{-1})	4713	2664	4790	4147	1156	6049

Table 2 Statistics for forest biomass (M_{tot}) (Mg ha^{-1}) and basal area (A_{tot}) (m^2 ha^{-1}) regressed against biomass-weighted mean community wood density (kg m^{-3}). The 2005 census is provided for the Luquillo plot, and analyses from other censuses showed similar patterns. Regressions were performed for a range of subcommunity sizes (Scale) (ha). Subcommunities were non-overlapping, resulting in a range of sample sizes (n). Ordinary least squares regression slopes are provided for significant correlations. Reduced major axis (RMA) regression overestimates the absolute value of regression slopes at low r^2 values (O'Connor *et al.*, 2007). Many of the significant correlations are characterized by low r^2 values. The RMA models are thus not reliable for this dataset, and we do not report RMA slopes.

Forest	Scale	n	M_{tot} vs. wood density			A_{tot} vs. wood density		
			P-value	r^2	Slope	*P*-value	r^2	Slope
Barro Colorado Island	2	25	0.03	0.15	−0.65	0.0005	0.39	−0.07
	1	50	0.06			0.0002	0.24	−0.06
	0.5	100	0.02	0.05	−0.36	< 0.0001	0.24	−0.06
	0.1	500	0.01	0.01	−0.24	< 0.0001	0.17	−0.07
	0.05	1000	< 0.0001	0.02	−0.35	< 0.0001	0.18	−0.08
Cocoli	1	4	0.3			0.6		
	0.5	8	0.4			0.7		
	0.1	40	0.2			0.0001	0.30	−0.11
	0.05	80	< 0.0001	0.19	−0.29	< 0.0001	0.47	−0.14
Sherman	1	5	0.12			0.11		
	0.5	10	0.08			0.25		
	0.1	55	< 0.0001	0.31	0.51	0.7		
	0.05	115	< 0.0001	0.21	0.57	0.25		
San Emilio	1	12	0.7			0.4		
	0.5	24	0.08			0.5		
	0.1	125	0.007	0.05	0.13	0.06		
	0.05	250	0.004	0.03	0.12	0.002	0.03	−0.02
Yasuni	1	25	0.14			0.8		
	0.5	50	0.01	0.11	1.03	0.2		
	0.1	240	0.02	0.02	0.34	0.4		
	0.05	500	0.002	0.02	0.34	0.3		
Luquillo	1	15	0.02	0.30	0.90	0.37		
	0.5	30	< 0.0001	0.49	1.0	0.03	0.13	0.04
	0.1	160	< 0.0001	0.36	0.85	< 0.0001	0.09	0.04
	0.05	320	< 0.0001	0.31	0.83	< 0.0001	0.08	0.04

The opposite relationships were observed in Luquillo, whereby forest biomass and total basal area both increased with community wood density, and these positive correlations were maintained across all four censuses. While forest biomass also increased with community wood density in Sherman, Yasuni and San Emilio, total basal area did not vary with community wood density in Sherman and Yasuni and declined weakly with community wood density in San Emilio (Table 2; Figs 1 & 2).

The slopes and explained variation of the forest biomass–community wood density and total basal area–community wood density linear regressions differed among forests and with subcommunity size within a forest. Slopes may be slightly shallower and explained variation may be slightly less at smaller spatial scales. These patterns were not, however, consistent among forests and the differences in slopes and explained variation were much greater among forests than across spatial scales within a forest (Table 2).

The direction of the total abundance–community wood density correlation was positive within Barro Colorado Island ($P = 0.06$, $r^2 = 0.11$) and Cocoli ($P = 0.01$, $r^2 = 0.07$), negative within Luquillo ($P \leq 0.005$, $r^2 \geq 0.23$, for all censuses) and non-

significant within Sherman, San Emilio and Yasuni. The direction of the maximum individual biomass–community wood density correlation was positive within Sherman ($P < 0.0001$, $r^2 = 0.31$), negative within Cocoli ($P = 0.004$, $r^2 = 0.09$) and was non-significant in Barro Colorado Island, San Emilio, Yasuni and Luquillo.

Annual precipitation, per area species richness, whole plot abundance and biomass were uncorrelated with slopes from forest biomass–community wood density and total basal area–community wood density regressions. Forest biomass–community wood density slopes were uncorrelated with, and total basal area–community wood density slopes increased strongly with, whole plot-level community wood density ($P = 0.019$, $r^2 = 0.73$). Slopes of the forest biomass–community wood density and total basal area–community wood density regressions within Luquillo did not vary as a function of time since the 1989 hurricane.

A positive relationship was observed between forest biomass–community wood density regression slopes and total basal area–community wood density regression slopes (all spatial scales and all four Luquillo censuses were included) (Fig. 3). This should not be taken as a valid regression, due to non-independence,
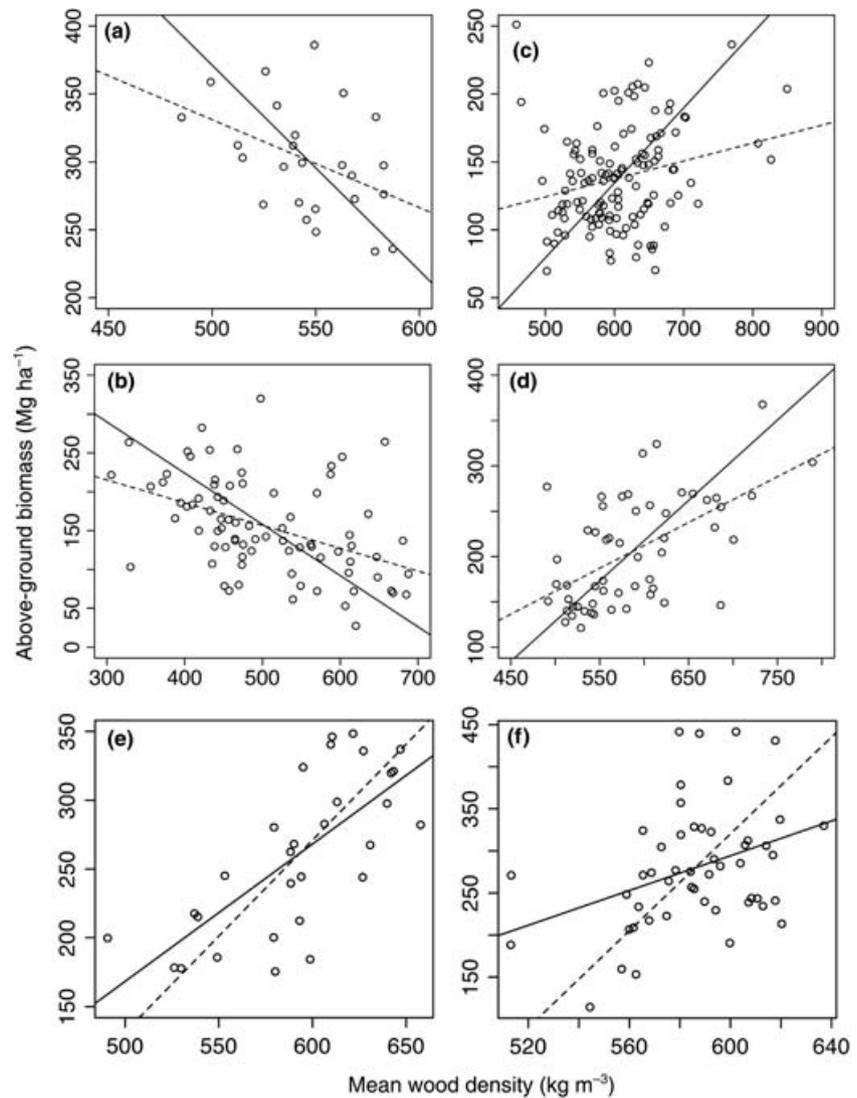
Figure 1 Above-ground forest biomass plotted against biomass-weighted mean community wood density for the best regressions (in terms of explained variance) for (a) Barro Colorado Island (2 ha), (b) Cocoli (0.05 ha), (c) San Emilio (0.1 ha), (d) Sherman (0.1 ha), (e) Luquillo, 2005 census (0.5 ha) and (f) Yasuni (0.5 ha) forest plots. Statistics for all spatial scales are provided in Table 2. Solid and dashed lines denote reduced major axis and ordinary least squares regressions, respectively. Note that axes are scaled differently for each forest.

but does qualitatively demonstrate that these correlations are positively related to each other.

DISCUSSION

In this paper we have broadened understanding of the relationship between forest biomass and community wood density. While it has been assumed that stand-level biomass increases with the wood density of constituent individuals, our analyses show that this is not generally true among the six tropical forests studied here. Forest biomass did not vary significantly with community wood density among forests and forest biomass–community wood density regressions varied from negative to null to positive within forests. Similar to previous work (Baker *et al.*, 2004), forest biomass increased with community wood density, but only in four (Sherman, San Emilio, Yasuni and Luquillo) of the six forests studied here (Table 2, Fig. 1), and only Luquillo was characterized by significant forest biomass–community wood density correlations at all subcommunity spatial scales. The subcommunity size that provided the best correlation (in terms of variation explained by community wood

density) differed between forests: 2 ha (Barro Colorado Island), 0.5 ha (Yasuni, Luquillo for all censuses), 0.1 ha (San Emilio, Sherman) and 0.05 ha (Cocoli). While the direction of significant correlations did not vary within a forest, at other spatial scales correlations were weaker and often non-significant. Clearly then, forest biomass is not consistently related to community wood density across forests or spatial scales and forest biomass does not generally increase with community wood density.

The six forests studied here differ in annual precipitation, whole plot-level community wood density and per area species richness, biomass and abundance (Table 1), which may explain differences in forest biomass–community wood density regression slopes. Regression slopes did not, however, vary significantly with any of these factors. The sign and magnitude of forest biomass–community wood density correlations within forests are instead determined, in part, by the underlying total basal area–community wood density correlation. Specifically, a positive correlation between forest biomass–community wood density and total basal area–community wood density linear regression slopes was observed (Fig. 3). This makes intuitive sense: basal area is intimately linked to standing biomass so that
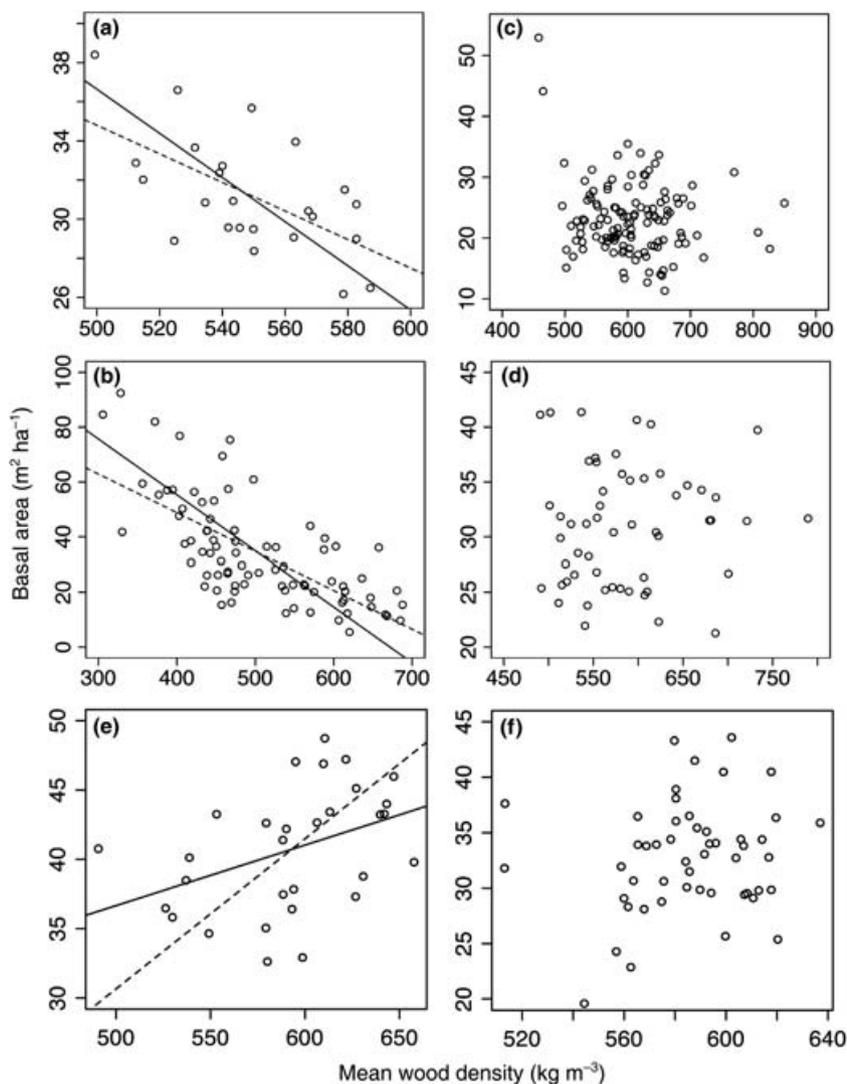
Figure 2 Total community-level basal area plotted against biomass-weighted mean community wood density for subcommunities in (a) Barro Colorado Island (2 ha), (b) Cocoli (0.05 ha), (c) San Emilio (0.1 ha), (d) Sherman (0.1 ha), (e) Luquillo, 2005 census (0.5 ha) and (f) Yasuni (0.5 ha). Statistics for all spatial scales are provided in Table 2. Solid and dashed lines denote reduced major axis and ordinary least squares regressions, respectively, for significant correlations. Note that axes are scaled differently for each forest.

an increase in basal area with wood density leads to an increase in biomass with wood density.

Although our analyses are not precisely the same as those performed by Baker *et al.* (2004), patterns demonstrated by these authors are generally consistent with our results. Baker *et al.* (2004) found that individual wood density did not vary with individual basal area, and that forest biomass increased with mean community wood density weighted by individual basal area. We similarly found forest biomass to increase with community wood density when total basal area did not vary significantly with community wood density. Our results and those of Baker *et al.* (2004) demonstrate that understanding the relationship between forest biomass and community wood density requires an understanding of what determines the sign and magnitude of total basal area–community wood density regressions.

Total basal area–community wood density regression slopes did not vary with annual precipitation, per area species richness, whole plot-level abundance or biomass, but did increase with whole plot-level community wood density. Hence, the greater the biomass dominance of high wood density species, the more positive the relationship between total basal area and community

wood density. Similarly, when forest biomass is dominated by low wood density species, total basal area declines with community wood density, and if this relationship is steep enough forest biomass will also decline with community wood density. This is the case in Barro Colorado Island and Cocoli (Tables 1 & 2). To understand the relationship between forest biomass and community wood density it would thus be useful to first understand what determines community wood density. High wood density can protect trees from xylem cavitation (Hacke *et al.*, 2001) so that it might be expected that the driest forests will have the highest community wood density. However, the forests in this study with the two highest community wood density values had the lowest (San Emilio) and highest (Luquillo) annual precipitation. While climate probably influences community wood density, additional factors are clearly important, and more work will be required to fully elucidate the factors that determine community wood density (see also Baker *et al.*, 2004).

In addition to whole plot-level community wood density, other factors must influence realized forest biomass–community wood density correlations. For example, within a forest, increasing subcommunity abundance and/or maximum tree size with
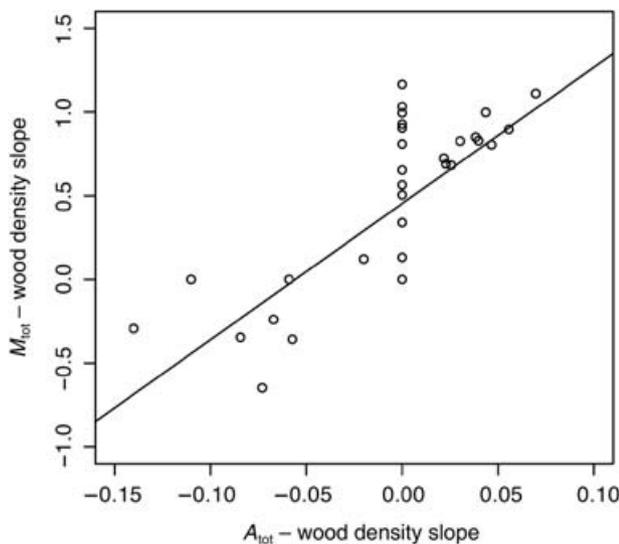
Figure 3 The ordinary least squares regression (OLS) slope for the correlation between forest biomass (M_{tot}) and biomass-weighted mean community wood density (BWWD) plotted against the OLS slope for the correlation between total community basal area and BWWD. A slope of zero is associated with non-significant correlations. All spatial scales from all forest plots, and all censuses for Luquillo, are used in the regression. As such, the assumption of independence is violated and we do not provide regression statistics.

subcommunity wood density may result in a more positive slope for the corresponding forest biomass–community wood density correlation. Indeed in Sherman, forest biomass and maximum individual biomass both increased strongly with community wood density. In addition, subcommunity abundance, maximum individual biomass and forest biomass either did not vary with or varied weakly with community wood density in San Emilio and Yasuni. In Cocoli and Barro Colorado Island, however, subcommunity abundance and maximum individual biomass appeared to have little influence over the decline in forest biomass with community wood density. Contrary to our expectations, although forest biomass increased strongly with community wood density in Luquillo, for all censuses, maximum individual biomass did not vary with and subcommunity abundance declined with community wood density.

The apparently conflicting pattern of increasing forest biomass and decreasing subcommunity abundance with community wood density in Luquillo is probably due to the intense disturbance history of Luquillo. Zimmerman *et al.* (1994) found that high wood density species preferentially survived the 1989 hurricane that disturbed the Luquillo forest, which should result in above-ground biomass being primarily held in high wood density trees. In turn, a strong increase in forest biomass with community wood density should emerge, as observed here. Furthermore, the number of individuals recruiting into a given subcommunity within Luquillo probably increased with severity of disturbance due to competitive release. Lower total abundance should thus be associated with the highest community wood density, as observed here. Disturbance events thus change how

wood density varies with tree size and how abundance and biomass are partitioned across the size distribution, which suggests that without ongoing disturbance, the relationship between forest biomass and community wood density within successional forests may show temporal trends. We did not, however, observe a temporal trend in the slope of the forest biomass–community wood density regression in Luquillo, but this is difficult to interpret due to a second, smaller hurricane event in 1998.

Although there is much yet to learn about what determines the magnitude and direction of forest biomass–community wood density correlations, quantifying this empirical relationship is important for the management of forests, especially in the context of global change. To provide useful management strategies, forest biomass–community wood density correlations should be carefully documented, as failing to do so may lead to suboptimal forest management. For example, Bunker *et al.* (2005) found a positive correlation between forest biomass and wood density for Barro Colorado Island via simulation analyses, and subsequently proposed plantations of high wood density species as a management strategy to increase carbon storage. A key factor to the proposed management strategy is their assumption that individual basal area does not vary with individual wood density. However, Chave *et al.* (2004) showed empirically, within the same forest studied in Bunker *et al.* (2005), that individual wood density declines with individual basal area. It has also been observed that within Amazonian forests, basal area and wood density show opposing patterns (Malhi *et al.*, 2006). These observations suggest that the assumption of basal area invariance with respect to wood density may be invalid and that the management strategy proposed by Bunker *et al.* (2005) may be counterproductive. Furthermore, we found forest biomass and/or total basal area to decline with community wood density among Barro Colorado Island, Cocoli and San Emilio subcommunities (Table 2; Figs 1 and 2), suggesting that the management strategy proposed in Bunker *et al.* (2005) would lead to *declines* in stored carbon.

Together, our results have important implications for the proposed decline in stored carbon as a result of declining wood density (Phillips & Gentry, 1994; Phillips *et al.*, 2002; Laurance *et al.*, 2006). Due to the negative association between forest biomass and community wood density in Barro Colorado Island and Cocoli, we suggest that in these (and similar) forests, factors selecting for lower wood density (e.g. increasing nitrogen deposition, solar radiation and/or atmospheric carbon dioxide) may act to increase stored carbon if basal area is maintained. More generally, the effect of declining community wood density on stored carbon can be roughly inferred from the underlying total basal area–community wood density correlation (Fig. 3), which can in turn be inferred from whole forest community wood density. The lower whole forest community wood density is currently, the stronger the current spatial decline in total basal area with community wood density, and the greater the potential increase in stored carbon with declining community wood density in the future.

In conclusion, it can no longer be assumed that the forest biomass increases with the wood density of constituent species or

that stored carbon will decline as a result of declining wood density. Extending our analyses across broader geographical extents and environmental gradients will help further elucidate the processes that determine how forest biomass is linked to wood density.

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