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Topographic and biotic regulation of aboveground carbon storage in subtropical broad-leaved forests of Taiwan

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ABSTRACT

There is a growing need to understand, and ultimately manage, carbon storage by forest ecosystems. Broad-leaved evergreen forests of Taiwan provide an outstanding opportunity to examine factors that regulate ecosystem carbon storage. We utilized data from three Taiwan Forest Dynamics Plots (FS, LHC, and PTY) in which every tree is identified, measured, tagged and mapped, to examine factors regulating carbon storage as estimated from aboveground biomass. Allometric equations were used to estimate the aboveground biomass of each tree, and a model building procedure was used to examine relationships between plot-level aboveground biomass (AGB; Mg/ha) and a suite of topographic and biotic factors. We found that our study sites have AGB values comparable to some of the most carbon dense forests in the world. Across all three sites, maximum biomass was contained in the taxonomic families Fagaceae, Lauraceae and Theaceae. In the FS site, we identified slope convexity ($P = 0.03$) and elevation ($P < 0.001$) as topographic predictors of AGB and found that maximum AGB was found in topographically flat areas. In FS, stem density ($P < 0.001$) was a significant biotic predictor of AGB and the maxima occurred at intermediate densities. In LHC, we found that convexity ($P < 0.001$) and slope ($P < 0.001$) were significantly related to AGB which was maximized along a topographic ridge in the plot. Species richness ($P < 0.001$) was a significant biotic predictor of AGB in LHC, and the relationship indicated slightly higher AGB at higher levels of species richness. The only significant factor related to AGB in PTY was species richness ($P = 0.02$). Further work is needed to seek a mechanistic understanding of topographic factors and species richness as drivers of carbon storage in forests.

1. Introduction

Increasing atmospheric carbon concentration is driving global climate warming, altering ecological systems worldwide (Solomon et al., 2007). Terrestrial ecosystems (Tans et al., 1990; Keeling et al., 1996), and forests in particular (Pregitzer and Euskirchen, 2004; Lewis et al., 2009; Keith et al., 2009), are critically important components of the global carbon cycle, transferring atmospheric carbon into storage pools. Forest management and preservation activities are increasingly taking into consideration the role of forests as carbon sinks (Li et al., 2007; Kirby and Potvin, 2007; Fahey et al., 2009), and there is a pressing need for more information about factors that determine carbon storage in forests (e.g., Birdsey, 1992; Mäkelä et al., 2000; Mascaro et al., 2005; Fahey et al., 2009).

Topographic and biotic factors are known to regulate carbon storage in forest ecosystems. Topographic characteristics such as elevation and aspect are known to drive patterns of tree species distribution (e.g., McEwan and Muller, 2006) and influence aboveground biomass (Valencia et al., 2009). For instance, de Castilho et al. (2006) found that topography played a significant role in determining live tree biomass in tropical forests of Amazonia, and elevation has been found to play a role in forest productivity in the Greater Yellowstone Ecosystem, USA (Hansen et al., 2000). Carbon storage in forests is also known to be related to biotic factors such as species diversity. Individual tree species have unique functional traits, such as specific leaf area and wood density that convey a particular capacity for carbon capture and sequestration (Brown et al., 1999; Kirby and Potvin, 2007; Chiang et al., 2008;

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Weishampel et al., 2009); thus, species rich forests may have an increased capacity for carbon storage (Kirby and Potvin, 2007).

Aboveground biomass (AGB) is an important carbon pool in forested ecosystems. Methods to estimate AGB within forests (Wenger, 1984), include direct estimation via vegetation destruction (Lin et al., 2001), remote sensing (Running et al., 2004), and computer simulations (Aber and Federer, 1992; Thornton et al., 2002). Forest dynamics plots (Losos and Leigh, 2004), in which detailed tree maps are established provide an incisive methodology for biomass estimation. Spatially-explicit information on individual trees over a large forested landscape allows for empirical assessment of the fine scale relationship(s) between aboveground biomass and local environmental factors (Chen et al., 2004). Such information is especially important for spatially heterogeneous habitats.

Taiwan, an island nation in southeastern Asia (Fig. 1), has developed a strong infrastructure for forest research with the development of the Taiwan Forest Dynamics Network, a suite of long-term forest monitoring plots (Lin and Wang, 2010). These plots were established following the sampling protocol defined by the Center for Tropical Forest Science (Lin and Wang, 2010) and provided an excellent opportunity to examine the factors driv-

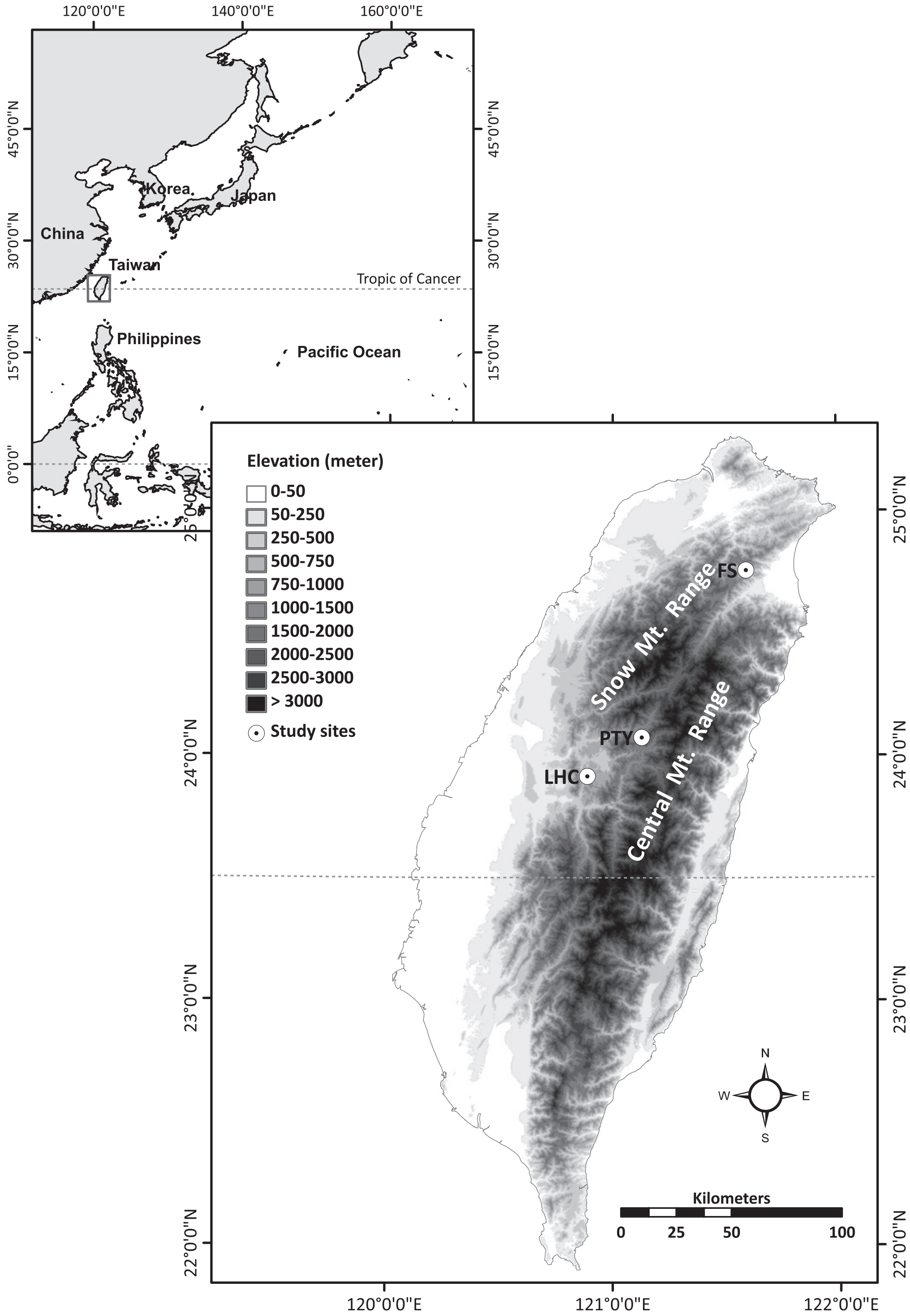

Fig. 1. Location of study sites on the island nation of Taiwan.

ing carbon capture in aboveground forest biomass. The island has extreme gradients in topography and landform variation leaves some forests vulnerable, and others protected, from the frequent typhoon disturbance the island experiences. These forests provide the opportunity to examine the biotic and abiotic factors that may govern carbon storage in topographically complex landscapes. We sought to advance understanding of the factors dictating aboveground biomass using three plots in the Taiwan Forest Dynamics Network. The first task in this project was to establish baseline AGB in our study sites and compare those values to other forest systems. We then assessed the relationship between aboveground biomass and both topographic and biotic factors. The overarching goal of our work is to develop a predictive and mechanistic framework for understanding carbon storage in these forests.

2. Methods

2.1. Study site description

This study focused on three plots in the Taiwan Forest Dynamics Network, all of which are dominated by broad-leaved evergreen forests that have never been extensively logged or plowed. Fushan Forest Dynamics Plot (FS; 24°45′ N, 121°35′ E) is a 25 ha (500 × 500 m) permanent plot in northern Taiwan (Fig. 1) with an average annual temperature and precipitation of 18.2 °C and 4271 mm, respectively (Su et al., 2007). A large quantity of precipitation at FS is from monsoon in winter and frequent typhoons in summer and elevation ranges from 600 to 733 m above sea level. The FS plot was censused in 2003–2004 by Taiwan Forestry Research Institute, Forestry Bureau, and National Taiwan University and 110 woody species were documented (Su et al., 2007). The dominant species include *Limlia uraiana*, *Castanopsis carlesii*, *Engelhardtia roxburghiana*, *Pyrenaria shinkoensis*, and *Meliosma squamulata* (Su et al., 2007).

Lienhuachih Forest Dynamics Plot (LHC; 23°54′ N, 120°52′ E) is a 25 ha (500 × 500 m) plot in central Taiwan that was established in 2007 by the Taiwan Forestry Research Institute (Fig. 1). Elevation in LHC ranges from 667 to 841 m and according to meteorological records in the research station from 1961 to 1998, the mean annual precipitation was 2211 mm, and was unevenly distributed through the year with a rainy season from March to September. According to the 2007–2008 census there are 144 species and 153,484 stems within the plot. Important canopy species include *Pasania nantoensis*, *Engelhardtia roxburghiana*, *Schefflera arboricola*, *Schima superba*, and *Cyclobalanopsis pachyloma* (Chang et al., 2010).

Mt. Peitungyen Forest Dynamic Plot (PTY; 24°05′ N, 121°08′ E) is a 3 ha (300 × 100 m) permanent plot located on a wide mountain ridgetop in central Taiwan (Fig. 1). This site is relatively well-protected from typhoon disturbance due to a natural barrier formed by the Central Mountain Range (Fig. 1). The elevation ranges from 1950 to 2055 m above sea level. A tree census of PTY plot was completed in the summer of 1996 (Song, 1996) and found 10,048 stems of woody trees greater than 1 cm DBH with a basal area of 78.72 m^2/ha. The most important species in the site are *Castanopsis carlesii*, *Barhtea barthei*, *Schima superba*, *Lithocarpus lepidocarpus*, and *Cinnamomum subavenium*. According to the weather stations at similar elevation nearby, the annual mean temperature was 13.0 °C (1996–2005) and the mean annual precipitation was 2657 mm (1992–2006; Hou, 2008).

2.2. Field sampling

The three plots were systematically divided into 20 × 20 m quadrats and, following Condit (1998), all woody stems with diameter at breast height (DBH) $\geqslant$1 cm were measured, tagged, mapped and identified to species. Convexity, elevation and slope were estimated for each of the quadrats (Harms et al., 2001; Valencia et al., 2004). Convexity was defined as elevation differences between the focal quadrat and mean elevation of the eight neighboring quadrats except for those quadrats on plot edges (Harms et al., 2001; Valencia et al., 2004). Positive values indicate convex surfaces, while concave surfaces would be associated with negative values (Harms et al. 2001; Valencia et al. 2004). Elevation was measured for each corner of the 20 × 20 m quadrat using a surveying theodolite. Slope was measured by the mean angular deviation from the horizontal plane of each of the four triangular planes by connecting three out of the four corners (Harms et al., 2001; Valencia et al., 2004). Within each plot, heights for trees $\leqslant$15 m tall were measured using measuring poles and trees >15 m tall were measured using a laser hypsometer.

2.3. Estimating aboveground biomass-model development

Chave et al. (2005) developed allometric models for the calculation of aboveground biomass from tree DBH and/or tree height for tropical forests. Because the forests of our study sites do not match precisely the conditions of the Chave et al. (2005) equations, we conducted a validation process. In particular, we compared equations for moist and wet forests in Chave et al. (2005), with and without height as an added variable. The Chave et al. (2005) models were as follows:

(1) Wet model including height: $AGB_{est} = \exp(-2.977 + \ln(\rho \times DBH^2 \times H))$.
(2) Wet model without height: $AGB_{est} = \rho \times \exp(-1.499 + 2.148 \times \ln(DBH) + 0.207 \times (\ln(DBH))^2 - 0.0281 \times (\ln(DBH))^3)$.
(3) Moist model with height: $AGB_{est} = \exp(-2.557 + 0.940 \times \ln(\rho \times DBH^2 \times H))$.
(4) Moist model without height: $AGB_{est} = \rho \times \exp(-1.239 + 1.980 \times \ln(DBH) + 0.207 \times (\ln(DBH))^2 - 0.0281 \times (\ln(DBH))^3)$.

In each model, ρ is wood density (g/m^3), DBH is the tree diameter at breast height (cm), and H is the tree height (m). These allometric equations were developed using datasets that only include trees with a DBH $\geqslant$ 5 cm. Although tree height of each individual stems were not measured, we measured the tree height for a subset of stems (679, 872, and 7695 stems for FS, LHC, and PTY, respectively) in each plot and derived site specific DBH (cm) and height (m) relationships using the following equation (Aiba and Nakashizuka, 2009):

(5) $H = H_{max} \times (1 - \exp(-a \times (DBH)^b))$.

In this equation, H_{max} is the asymptotic maximum height and a and b are constants. H_{max}, a, and b were estimated by fitting the equation above with the observed DBH and height of the selected stems. Simulated annealing (Goffe et al., 1994) with maximum iterations of 20,000 was used to attain optimized model fit (using "anneal" function of likelihood package in R statistical software; Development Core Team, 2010; Charles D. Canham, personal communication). Site specific tree height-DBH relationships were used to estimate tree height of each individual stems using DBH.

Chave (personal communication) suggested that tree height could introduce important variation into our biomass estimates. Therefore, we tested the accuracy and precision of the allometric models both with, and without, estimated tree height. For this analysis, we obtained aboveground biomass data of 96 individual trees in Fushan site (raw data from Lin et al., 2001). We used the DBH and species information that was associated with this dataset and applied each equation, both with and without estimated tree height. We assessed model efficiency (EF; Mayer and Butler, 1993) using the following equation:

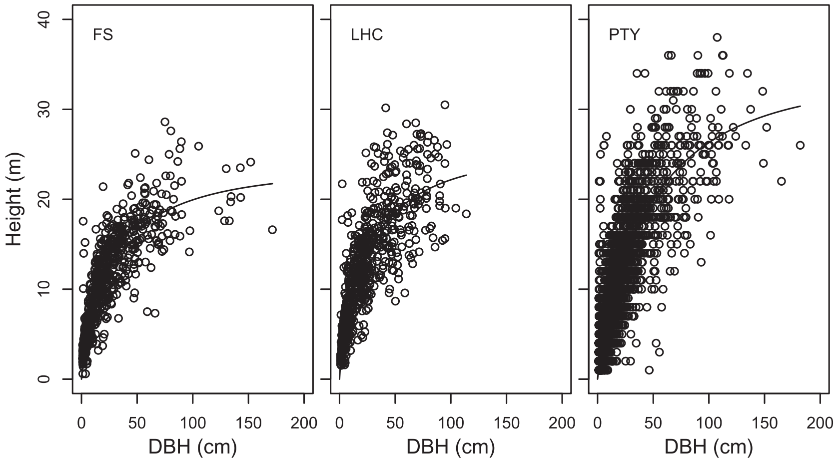

Fig. 2. The relationship between tree height (m) and DBH (cm) in three broad-leaved evergreen forests in the nation of Taiwan: Fushan (FS), Lienhuachih (LHC), and Mt. Peitungyen (PTY) research sites.

(6)

$$EF = 1 - \left(\sum (y_i - \hat{y}_i)^2\right) \Big/ \left(\sum (y_i - \bar{y}_i)^2\right) \tag{1}$$

In this equation, y_i is the observed value, $\hat{y}_i$ is the estimated value, and $\bar{y}_i$ is the mean of the observed value of AGB. EF is similar in interpretation to a R^2 value, but rather than measuring deviation from a best fit line, EF measures deviation from a 1:1 line (i.e., a perfect fit). When calculating each of the equations, between-species differences were accounted for by wood density. Wood density data were obtained from the Global Wood Density Database (Chave et al., 2009). We first calculated mean wood density for each species, genus, and family in the database. Wood density for each stem in the census was matched to the species mean calculated from the Global Wood Density Database. If species level data were not available, genus level or family level data (decreasing priority) were used. Wood density is highly conserved within a genus (Swenson and Enquist, 2007). Wood density data of genus or species level were available for 77.8%, 61.6%, and 67.5% of stems in LHC, FS, and PTY, respectively.

2.4. Analysis

We used generalized least squares regressions (GLS) to investigate the relationship between AGB and both biotic (species richness and stem density) and abiotic (elevation, slope, and topographic convexity) variables. The GLS model was chosen to accommodate spatial autocorrelation among quadrats (Schabenberger and Gotway, 2005). To identify important predictors, a best-fit model for each site was developed. To construct the best-fit model, factors were sequentially eliminated from the full models until all factors in the model were significant. If there were several possible models, the model with the smallest value of Akaike's Information Criterion (AIC) was chosen. The best-fit models for all sites were significantly improved from the null models (see Appendix A). The full model contained quadratic and linear terms of the above five factors. To avoid collinearity among predictors, we constructed an additional set of GLS models to explore the relationships between species richness and the other four predictors. This set of GLS models indicated that species richness was significantly correlated with the number of individuals in all of the study sites, but only significantly with convexity^2 in LHC and elevation in PTY. As a result, convexity^2 was excluded from the final model since it was not as significant as species richness in the full model. In PTY, neither elevation nor elevation^2 were significant in the full model so that they were not included in the final model. Parameters were estimated using maximum likelihood methods. The models were performed by the R package, nlme (Pinheiro et al., 2009).

3. Results

3.1. Forest structural characteristics

Tree height in our study sites ranged to nearly 40 m in PTY and many tree diameters were >100 cm in all three sites (Fig. 2). The relationship between height and diameter was curvilinear and asymptotic leveling off near 20 m in FS and LHC. Trees were substantially taller in PTY with the relationship flattening near 30 m (Fig. 2). Size-class relationships were similar in the three study sites and were characterized by sharp inverse-J relationships and density in the smallest size class was highest in LHC (see Appendix B, Fig. B1).

3.2. Estimating aboveground biomass

The accuracy of both moist and wet models proposed by Chave et al. (2005) for tropical forests was significantly improved by the incorporation of tree height into the model (Fig. 3). Our analysis included the Chave et al. (2005) model for both moist and wet tropical forest (Fig. 3, first and second rows of panels, respectively). Without the inclusion of tree height, each model predicted biomass well at low levels, but substantially overestimated biomass at higher biomass (Fig. 3b and d). With the inclusion of height into the model, the model predictions were much more accurate at higher biomass (Fig. 3a and c). Efficiencies for the moist (EF = −0.43) and wet (EF = 0.66) models without height as a factor were substantially lower than those derived using tree height as a factor (EF = 0.85 and 0.83, for moist and wet, respectively). Due to the results of this validation process we conclude that tree height is an important parameter and we included height for the estimation of AGB in all analyses. We present both models for comparisons with other studies (Section 3.3 below), but otherwise present only model results based on the moist forest equation including height as it yielded the most accurate prediction.

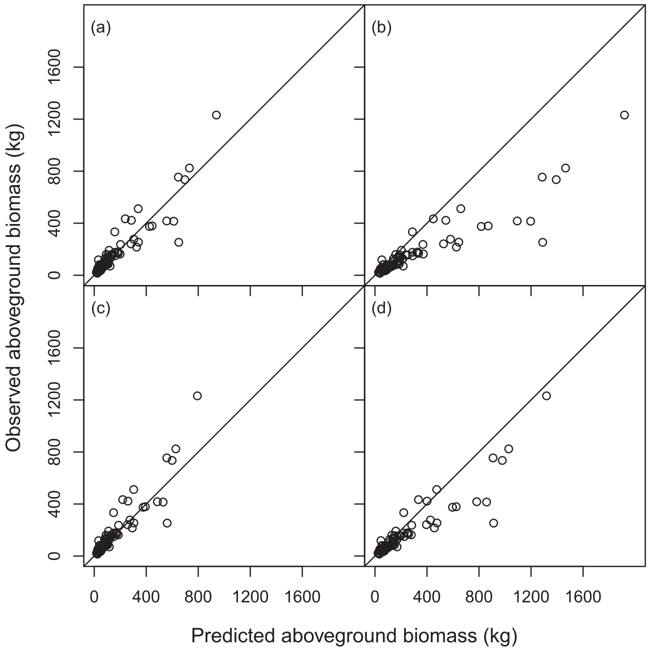

Fig. 3. Validation of four allometric models in broad-leaved evergreen forests of the Fushan (FS) research site in northeastern Taiwan. Observed aboveground biomass was obtained from the aboveground biomass data of 96 individual trees sampled in FS. Predicted aboveground biomass was estimated by four respective allometric functions suggested by Chave et al. (2005): (a) allometric function with tree height input for moist forest; (b) allometric function without tree height input for moist forest; (c) allometric function with tree height input for wet forest; (d) allometric function without tree height input for wet forest.

3.3. Aboveground biomass comparison

Our study sites have AGB values comparable to some of the most carbon dense forests in the world (Fig. 4). Model predictions using moist and wet allometric equations produced very similar results for LHC and FS, each of which had median values comparable to the Hubbard Brook Experimental Forest in North America, and slightly higher than some plantation forests of Taiwan (Fig. 4). There was some variation among wet and moist allometric equations in predicting PTY biomass; however, both models suggest this site had carbon values that were in the upper range of forests we examined (Fig. 4). Despite differences among sites in total AGB, the values were similarly distributed along taxonomic families (Appendix B, Fig. B2). The highest values in all three sites were found in the Fagaceae. The AGB represented by this family varied widely among sites, with values ranging from nearly 350 Mg/ha in PTY to just less than 60 Mg/ha in LHC. Lauraceae and Theaceae were second and third most important, respectively, in all three sites (Appendix B, Fig. B2).

3.4. Abiotic and biotic predictors of aboveground biomass

Factors that were significant predictors of AGB differed among sites and included topographic and biotic variables. In FS (top row of panels, Fig. 5), we found that the topographic variables convexity and elevation were significantly related to AGB (Table 1). In particular, AGB was maximized at a convexity value near zero (topographically flat; Fig. 5a) and at elevations just over 650 which is a relatively low value for the site (Fig. 5b). These relationships were supported by the fact that a topographic peak in lower left quadrant of the FS plot was an area of high convexity and low AGB (Fig. 6). Stem density was also a significant predictor of AGB in FS, with an obviously positive relationship at low densities followed by a peak and then decline at the highest densities (Fig. 5c). In fact, in the FS site, a significantly curvilinear relationship between AGB and stem density was detected (Fig. 5c and Table 1). In the LHC site (second row of figures, Fig. 5), convexity, slope, and species richness were significantly related to AGB (Table 1). A ridge in the center of the LHC plot, where convexity is maximized, contained areas of maximum AGB (Fig. 6). In PTY,

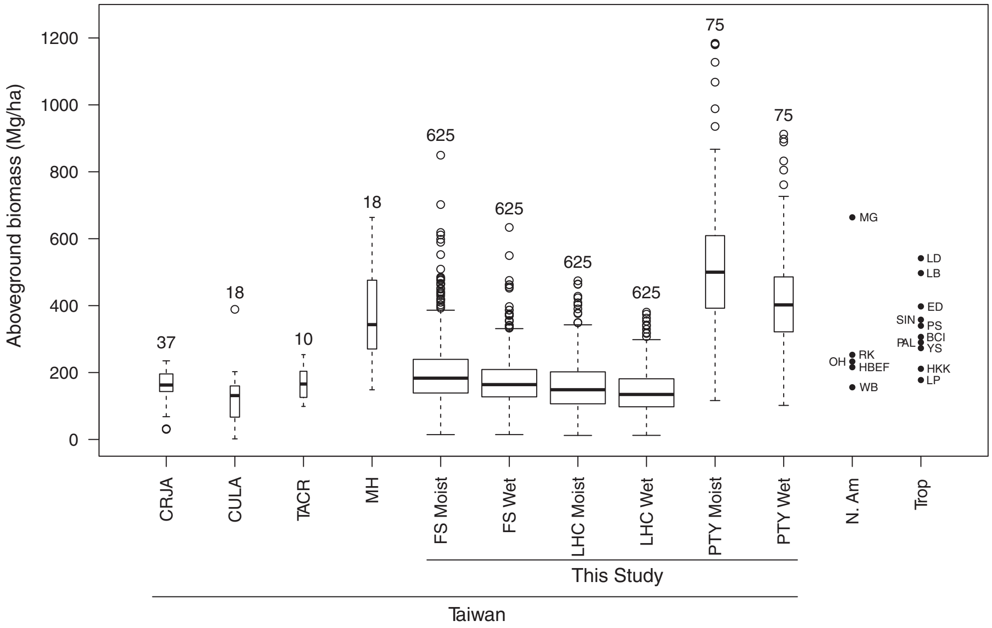

Fig. 4. Estimated aboveground biomass of various forests worldwide. Sources of data are listed in Appendix C. Acronyms of categories are described as follows, CRJA: *Cryptomeria japonica* plantation; CULA: *Cunninghamia lanceolata* plantation; TACR: *Taiwania cryptomerioides* plantation; MH: Mixed hardwood forests; N. Am.: Forests of North America; Trop: Tropical rain forests. Acronyms of site names in the plot regions are described as follows, BCI: Barro Colorado Island, Panama; ED: Edoro, Democratic Republic of Congo; FS: Fushan Experimental Forest, Taiwan; HBEF: Hubbard Brook Experimental Forest, United States; HKK: Huai Kha Khaeng, Thailand; LB: Lambir, Malasia; LD: Lenda, Democratic Republic of Congo; LHC: Lienhuachih Experimental Forest, Taiwan; LP: La Planada, Colombia; MG: Munger Research Natural Area, United States; OH: Ohio Hills sites of the Fire and Fire Surrogate Study, United States; PAL: Palanan, Philippines; PS: Pasoh, Malasia; PTY: Mt. Peitungyan, Taiwan; RK: Rocky Mountain National Park, United States; SIN: Sinharaja, Sri Lanka; WB: Walker Branch Forest, Oak Ridge, United States; YS: Yasuni, Ecuador.

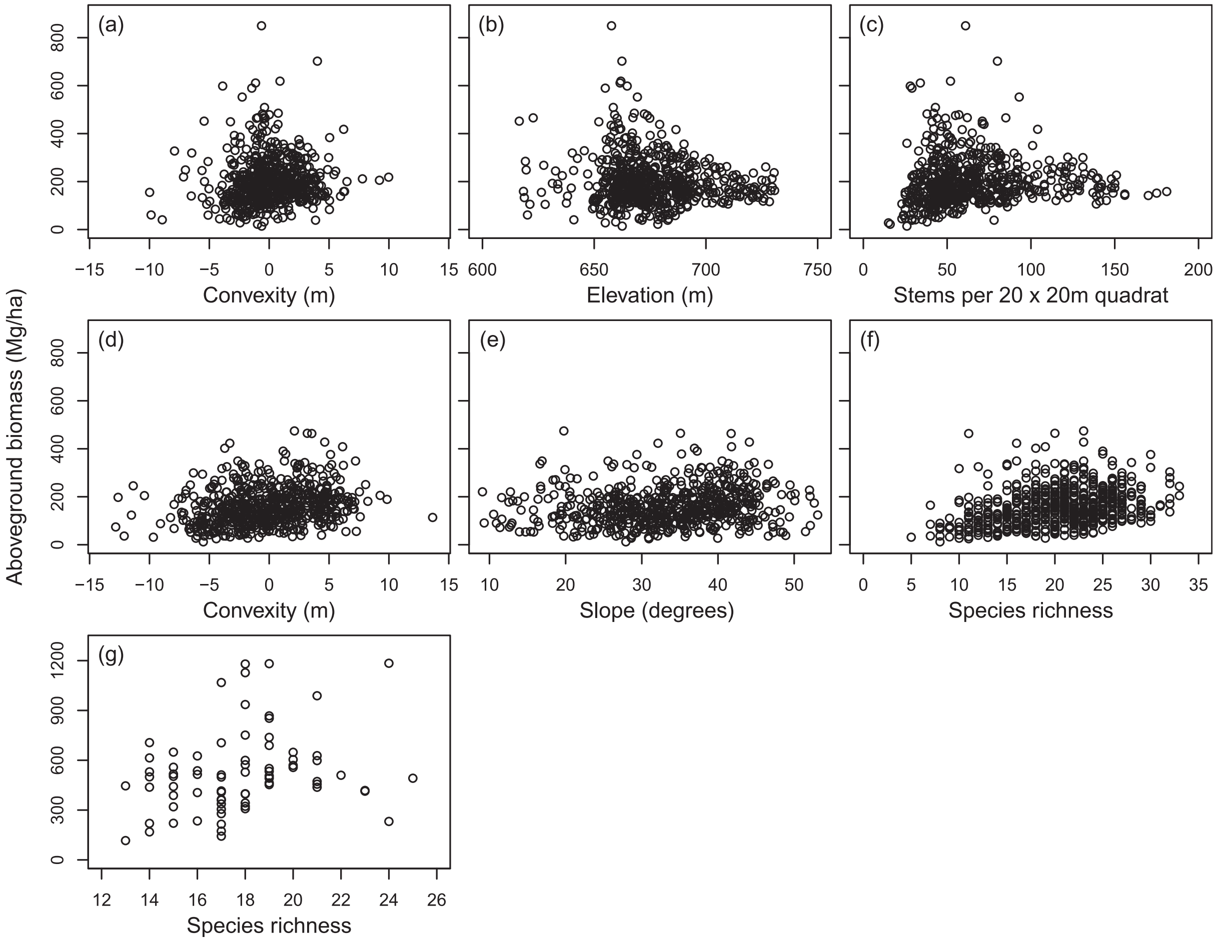

Fig. 5. Scatter plots demonstrating relationships between aboveground biomass and significant predictors from the best-fit generalized least squares regressions (GLS) in Fushan (FS; a–c), Lienhuachih (LHC; d–f), and Mt. Peitungyen (PTY; g) research sites in the nation of Taiwan.

the only significant factor detected by the analysis was species richness (Fig. 5g and Table 1). This relationship was apparently positive until species richness reached 20 (Fig. 5g).

4. Discussion

4.1. Aboveground biomass in subtropical forests of Taiwan

The influence of atmospheric carbon on climate is an ever more pressing global issue and carbon sequestration is an increasingly important concern for forest management. Attention has focused on the role of tropical forests as carbon sinks (e.g., Vieira et al., 2004; Baker et al., 2004; Lewis et al., 2009) and recent work has suggested that mid-latitude broad-leaved forests also have considerable potential for biomass accumulation (Pregitzer and Euskirchen 2004; Keith et al. 2009). Forests in our three study sites have AGB levels comparable to some of the most carbon-dense forests worldwide (Brown et al., 1999; Pregitzer and Euskirchen, 2004; Keith et al., 2009). Old-growth forests are known to serve as carbon sinks (Luyssaert et al., 2008), and PTY which is old-growth forest and topographically protected from typhoon disturbance, had biomass volumes that were comparable to any of the forest types we examined across the globe. This strongly suggests (1) that old-growth subtropical hardwood forests have the capacity for extremely high levels of biomass accumulation, and (2) that for Taiwan, in particular, broad-leaved forests that are managed for development into old-growth status have the potential for substantial carbon storage.

4.2. Topography and disturbance as controls on aboveground biomass

Topography is known to influence forest composition and biomass (e.g., Whittaker, 1956). Across topographic gradients, biomass accumulation is known to be associated with soil resources (McEwan and Muller, 2006; de Castilho et al., 2006; Paoli et al., 2008). In our study sites, we found significant relationships between AGB and a variety of topographic variables, including slope convexity. These relationships could be related to nutrient availability (which we did not measure). For instance, the relationship between slope convexity and AGB at high elevations may be partially explained by topographically related changes in soil quality. Further work is needed to investigate this possibility.

Disturbance is another factor that is known to drive AGB patterns, and in our study, variation of biomass associated with topography may be related to typhoon disturbance. The island nation of Taiwan experiences significant typhoons each year, and these storms have substantial impacts on forests. Disturbance is an important influence on ecosystem carbon storage (e.g., Rice et al., 2004; Mascaro et al., 2005; Running, 2008) and may have influenced patterns of AGB in our sites. The PTY site is topographically protected from typhoon disturbance by the Central Mountain Range and this site had vastly larger AGB than the other two sites, even though these forests are similar in composition and in the distribution of existing biomass among taxonomic families. We hypothesize that this difference is at least partially related to the fact that FS and LHC are more exposed to typhoon disturbance. In FS, previous research has clearly demonstrated that strong wind

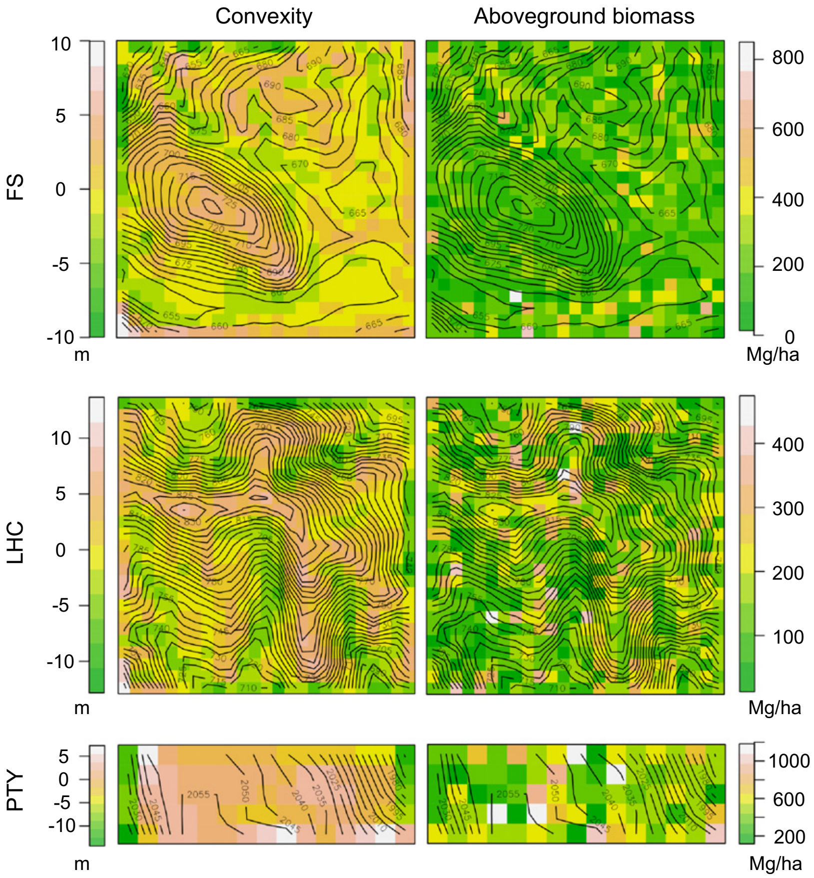

Fig. 6. Spatial variability in convexity (see text for details) and aboveground biomass in three broad-leaved evergreen forests of Taiwan. Each color pixel represents a 20 × 20 m quadrat and the contour lines are in 5-m intervals.

Table 1
Results of the best-fit generalized least squares regressions (GLS) exploring relationships between aboveground biomass (AGB) and both topographic and biotic variables in three evergreen hardwood forests of Taiwan (FS: Fushan; LHC: Lienhuachih; PTY: Mt. Peitungyen). See text for explanations of the variables.

Site	Variable	Estimate	SD	*t*	*P*
FS	Convexity	4.319	2.003	2.156	0.0315
	Elevation	−1.177	0.247	−4.770	<0.0001
	No. of stems^2	−0.012	0.003	−3.501	0.0005
	No. of stems	2.415	0.592	4.079	0.0001
LHC	Convexity	3.841	0.804	4.780	<0.0001
	Slope	1.270	0.345	3.677	0.0003
	Species richness	3.350	0.583	5.749	<0.0001
PTY	Species richness	23.738	10.236	2.319	0.0232

The pseudo-R^2, estimated based on Griffis and Stedinger (2007) for the best-fit models of FS, LHC, and PTY sites are 0.07, 0.14, and 0.07, respectively.

brought by typhoons plays an important role in the dynamics of canopy leaf area index, stand structure, and nutrient cycling (Mabry et al., 1998; Lin et al., 2003; Lin et al., 2011). In FS, maximum AGB was found in flatter areas, which are less exposed to wind and less susceptible to landslides. In LHC, the major mode of disturbance brought by typhoons is not wind, but instead, heavy precipitation, which leads to landslides and temporary flooding (Li-Wan Chang, unpublished data). This may have been the reason why maximum AGB in LHC was found on upper elevation sites that were convex. Typhoon disturbance is known to influence ecosystem carbon accumulation and storage (Mascaro et al., 2005) and, like other disturbance processes, will tend to drive carbon out of the living biomass pool and increase the amount of standing dead biomass and coarse woody debris (Rice et al., 2004; Running, 2008). Our work suggests that typhoons may also directly alter aboveground biomass in forests. In particular, (1) within sites that are exposed to typhoons, the topographically exposed areas accumulate the least AGB, and (2) among otherwise similar sites, persistent typhoon disturbance can place a strong limitation on AGB accumulation. Further work is needed to vet these ideas and to explore the potential role of topography as a surrogate for disturbance exposure in complex landscapes.

4.3. Biodiversity and aboveground biomass

The relationship between diversity and productivity has been an important source of discussion in ecology (e.g., Grime, 1973; Huston, 1979; Oksanen, 1996; Grace, 1999). Recent work has reframed this issue to focus on questions of biodiversity and ecosystem function (e.g., Stachowicz et al., 2002; Bunker et al., 2005; Fornara and Tilman, 2009). An increasingly pertinent question for forest managers is whether the most diverse forests are also those that sequester the most carbon (Kirby and Potvin, 2007). We found that species richness, but not density, was a significant predictor of AGB in both LHC and PTY. This suggests that functional complementarity among species may be a factor in the accumulation of AGB in these sites. In the FS site, stem density was related to AGB in a significantly unimodal fashion. This pattern matches the well-known, and often debated, "humped" relationship between biodiversity and productivity (Huston, 1979; Oksanen, 1996; Grace, 1999). Future work is needed to seek evidence of among-species functional complementarity and to explore the role of biodiversity as a driver of carbon storage along resource gradients in these forests.

4.4. Forest complexity and carbon storage in evergreen broad-leaved forest

Broad-leaved evergreen forests in Taiwan may be among the most carbon rich ecosystems in the world. The forests of Taiwan are ideal for exploring AGB storage because these forests are species rich, topography is complex, and disturbance regimes are variable across the island. In our study, AGB was strongly related to forest species diversity and topographic variation. We postulate that disturbance shapes the distribution of AGB and that topography plays a primary role in mediating the influence of typhoons which regularly buffet the island. Future work is needed to test these hypotheses, and elucidate the complex drivers of carbon accumulation in these forests.

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Appendices Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2011.07.028.

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