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Relationship Between Aboveground Biomass and Multiple Measures of Biodiversity in Subtropical Forest of Puerto Rico

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ABSTRACT

Anthropogenic activities have accelerated the rate of global loss of biodiversity, making it more important than ever to understand the structure of biodiversity hotspots. One current focus is the relationship between species richness and aboveground biomass (AGB) in a variety of ecosystems. Nonetheless, species diversity, evenness, rarity, or dominance represent other critical attributes of biodiversity and may have associations with AGB that are markedly different than that of species richness. Using data from large trees in four environmentally similar sites in the Luquillo Experimental Forest of Puerto Rico, we determined the shape and strength of relationships between each of five measures of biodiversity (*i.e.*, species richness, Simpson's diversity, Simpson's evenness, rarity, and dominance) and AGB. We quantified these measures of biodiversity using either proportional biomass or proportional abundance as weighting factors. Three of the four sites had a unimodal relationship between species richness and AGB, with only the most mature site evincing a positive, linear relationship. The differences between the mature site and the other sites, as well as the differences between our richness–AGB relationships and those found at other forest sites, highlight the crucial role that prior land use and severe storms have on this forest community. Although the shape and strength of relationships differed greatly among measures of biodiversity and among sites, the strongest relationships within each site were always those involving richness or evenness.

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Key words: diversity; dominance; evenness; Luquillo Experimental Forest; rarity; species richness.

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ANTHROPOGENIC CHANGE THREATENS BIODIVERSITY WORLDWIDE (Sala *et al.* 2000, Andelman & Willig 2003), and is increasing at an accelerating rate (Vitousek *et al.* 1997, Carney *et al.* 2004). In these times of anthropogenic change, the Caribbean is of particular interest as it is a hotspot of biodiversity (Connell 1978, Rosenzweig 1995, Blackburn & Gaston 1996, Presley & Willig 2008, Willig *et al.* in press) and is a region with intense human activity (Ellison & Farnsworth 1996, Ortiz-Zayas *et al.* 2006). An important goal in ecology is to understand the structure of such communities by describing their biodiversity and biomass, and quantifying relationships between them (Hooper *et al.* 2005, Keddy 2005).

In the past 25 yr, interest has increased dramatically in determining the relationship between biodiversity and various ecosystem functions. One of the most commonly studied relationships is that between species richness and productivity, or its surrogates (see Waide *et al.* 1999, Mittelbach *et al.* 2001 for additional references). Much of this productivity–species richness research has focused on grasslands, in part because biomass can be removed easily on an annual basis to estimate productivity. Considerably fewer studies examine productivity–species richness relationships in forests, perhaps because of the difficulty of using biomass as a surrogate for productivity in long-lived trees. However, describing the relationship between species richness and biomass in forests is useful outside the context of productivity. For example, it is necessary to understand this relationship to determine how biomass may accrue in monocultures or tree plantations compared with native forests (Lugo 1992, Piotto *et al.* 2004, Erskine *et al.* 2006, Potvin & Gotelli 2008); make inferences about the carbon storage potential of forests differing in species richness (Caspersen & Pacala 2001); and develop hypotheses about mechanisms driving this relationship (Hooper *et al.* 2005). These questions are particularly relevant for forests identified as biodiversity hotspots, like the Caribbean, that are being heavily influenced by human activity. We strive to add to the knowledge base on this important topic by using a data set from Luquillo Experimental Forest (LEF) in Puerto Rico to examine the relationship between AGB and species richness in a subtropical forest.

Considerable controversy surrounds the relationship between species richness and biomass, in part because a unimodal pattern was heralded by some as the 'true' (Rosenzweig 1992) or most pervasive (Huston & DeAngelis 1994) relationship. Nonetheless, a broad survey of the literature, including a meta-analysis of empirical patterns (Mittelbach *et al.* 2001), revealed that unimodal relationships are not the sole or most pervasive pattern under all circumstances. Limited evidence for forests suggests that unimodal patterns are less typical for long-lived trees than for short-lived herbaceous plant communities.

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For forest communities, positive (Caspersen & Pacala 2001, Erskine *et al.* 2006, Sagar & Singh 2006, Houle 2007, Vila *et al.* 2007), negative (Lugo 1992, Wardle *et al.* 1997), and no relationships (Vila *et al.* 2003) between biodiversity and AGB have been documented.

Although results are not consistent regarding the relationship between species richness and AGB in forests, results are more uniform regarding how AGB differs between monocultures in plantations and mixed-species plots. Trees grow faster and attain greater biomass in mixtures than in some monocultures (Piotto *et al.* 2004, Erskine *et al.* 2006, Potvin & Gotelli 2008), although mixtures do not always outperform the best monocultures (Lugo 1992, Piotto *et al.* 2004). Therefore, positive relationships may be the most obvious initial expectation for the relationship between species richness and AGB.

Using forest data from the LEF, we expand the discussion of the relationship between biodiversity and AGB to include measures of biodiversity beyond species richness. Although most of the research addressing the association between biodiversity and AGB has used species richness as the measure of biodiversity (Giller *et al.* 2004), biodiversity comprises multiple components (*e.g.*, richness, evenness, dominance, rarity), and various indices weight such components differently. Often, an implicit assumption is that richness is highly correlated with other measures of biodiversity, and that by examining richness–AGB relationships, salient features are revealed about the biodiversity–AGB relationship. Empirical support for this proposition is equivocal. For example, a high correlation exists between Shannon–Weiner diversity (H') and species richness across tropical forests (Gentry 1988), but only moderate correlations occur between Shannon diversity and species richness or between Simpson's diversity and species richness in planktonic foraminiferal assemblages (Berger & Parker 1970). Indeed, richness and evenness are not necessarily correlated (Stirling & Wilsey 2001, Stevens & Willig 2002, Wilsey *et al.* 2005) and can contribute to biodiversity in distinctive ways (Buzas & Hayek 1996). Thus, additional studies of the relationship between multiple measures of biodiversity and AGB are needed to distinguish general patterns from site-specific circumstances (Buzas & Hayek 1996, Nijs & Roy 2000, Giller *et al.* 2004, Olszewski 2004, Chalcraft *et al.* 2009).

Previous work examining the relationship between multiple aspects of biodiversity and AGB has not yielded consistent results. Shapes of the relationships between a number of measures of biodiversity and AGB were extremely variable among several long-term grassland sites, and the strengths of association were often quite weak (Chalcraft *et al.* 2009). A significant negative relationship between Shannon diversity and biomass existed in Michigan old-fields, but only in one of 7 yr; no significant relationship occurred in the other years (Huberty *et al.* 1998). In contrast, total biomass increased linearly with increasing evenness in a Quebec old field (Wilsey & Potvin 2000). An inevitable conclusion from these studies is that multiple components of biodiversity should be used to explore the relationship (Buzas & Hayek 1996, Nijs & Roy 2000, Olszewski 2004).

Here, we use the LEF forest inventory data to examine the influence of weighting biodiversity indices by relative biomass vs. abundance. Early theoretical work concerning indices of biodiversity stressed that weighting may be achieved with any of a number of measures of importance (Pielou 1975). In empirical studies, measures of biodiversity involve weighting by relative biomass (*e.g.*, Mulder *et al.* 1999, Wilsey & Potvin 2000, Chalcraft *et al.* 2009) or by relative abundance (*e.g.*, Stevens & Willig 2002). Typically, studies in grasslands involve weighting by relative biomass (Tilman *et al.* 2001, Caldeira *et al.* 2005), whereas studies on trees or animals weight richness by relative abundance (Huston 1980, Phillips *et al.* 1994, Amarasekare 2003). In grassland systems, weighting is related to sampling protocols; herbaceous vegetation is clipped at the end of the growing season with no way to distinguish individuals. The extent to which conclusions based on weighting by proportional biomass differ from those weighting by proportional abundance is unknown.

This paper is the first known effort to examine relationships between multiple components of biodiversity and AGB based on weighting by relative biomass as well as by relative abundance. Using data from environmentally similar plots in the same forest type within LEF, a subtropical wet forest (*sensu* Holdridge 1967) in Puerto Rico, we determine the shape and strength of the relationship between each of five measures of biodiversity (species richness, Simpson's diversity, Simpson's evenness, rarity, and dominance) and AGB, and examine differences in relationships when richness is weighted by proportional abundance rather than by proportional biomass.

METHODS

The International Institute of Tropical Forestry (IITF) has collected data on the temporal and spatial dynamics of tropical trees in eastern Puerto Rico since 1939 (Wadsworth 1970, Brown *et al.* 1983, Weaver 1983, Zimmerman *et al.* 1994). In one of these efforts, Wadsworth established a number of long-term representative forest plots in each of four areas (*i.e.*, Sabana 4, Sabana 8, Cubuy, and Río Grande) within the Luquillo Mountains. Within each site, a systematic sampling design of plots was established (Parresol & Alemañy 1998). Wadsworth's purpose was to compare growth rates of crop trees in sites exposed to selective tree removal with those in sites with no removals. The removal treatment was applied once in 1958. Plots were sampled periodically (every 10–15 yr) to evaluate site-specific and species-specific growth rates (Crow & Weaver 1977, Parresol & Alemañy 1998). Although collected for such purposes, we use these data to address questions concerning the relationship between aspects of biodiversity and AGB. Consequently, the design of data collection was not without shortcomings with respect to our goals (see Appendix S1).

STUDY AREAS.—We selected four sites (Sabana 4, Sabana 8, Cubuy, and Río Grande; Table 1) in the LEF to represent subtropical wet forest or tabonuco forest, named for the dominant tree, *Dacryodes excelsa*. The sites are characterized by deep, acid, clay soils, uneven terrain, mean annual temperatures of 22–24.2°C, and mean annual precipitation of 2000–4000 mm (Crow & Weaver 1977, Silver *et al.* 2004). Sabana 4 comprises mature forest on the eastern side of the LEF that has never been cultivated or used as pasture (Crow & Weaver 1977). Its most abundant large trees are *D. excelsa*, *Sloanea berteriana*, and *Inga laurina*. Sabana 8 represents secondary forest

TABLE 1. *Descriptions of the four study sites in the Luquillo Experimental Forest of Puerto Rico. Each plot had an area of 809.3 m*^{2}. *Site size describes the area of the tract of forest with a given site name in which these plots were located.*

Site name	Latitude	Longitude[a]	Elevation (m)[a,b]	Successional status[b,c]	Mean tree density (number/plot)	Mean basal area (m^2/plot)	Site size (ha)[a,c]	Number of plots
Sabana 4	18°25′ N	65°43′ W	300–600	Mature	9.4	262.63	129	85
Sabana 8	18°19′ N	65°42′ W	200–400	Secondary	10.4	198.42	80	83
Río Grande	18°17′ N	65°50′ W	450–650	Secondary	13.4	275.03	40	70
Cubuy	18°16′ N	65°54′ W	300–600	Secondary	12.4	216.92	105	73

[a] S. Alemañy (unpubl. data).
[b] Parresol & Alemañy (1998).
[c] Crow and Weaver (1977).

on the eastern side of the LEF that was farmed before 1947 (Crow & Weaver 1977). Its three most abundant large trees are *Tabebuia heterophylla*, *Alchornea latifolia*, and *I. laurina*. Río Grande also represents secondary forest and is on the western side of the LEF that was used as pasture land, but probably was not cultivated extensively (Crow & Weaver 1977). *Dacryodes excelsa*, *T. heterophylla*, and *Matayba domingensis* are the most abundant large trees. Finally, Cubuy contains secondary forest on the western side of the LEF that was pasture land before the 1930s (Silver *et al.* 2004). *Tabebuia heterophylla*, *Tectona grandis*, and *Calophyllum antillanum* are the most abundant large trees.

SAMPLING DESIGN.—Each plot was a 0.08 ha circle (16.05 m radius) and each site contained over 100 plots. However, we limited analyses to plots for which all trees > 24.2 cm dbh were identified to the specific level (Table 1) and measured in 1991–1992 (the most recent measurement of these plots). The number of plots we used varied by site, ranging between 70 and 85 plots (Table 1). Although this analysis does not include many smaller trees, we were restricted by our data set, which was only complete for trees > 24.2 cm dbh; many of the smaller trees in the plots were not measured.

AGB.—We used species-specific allometric equations developed for the tabonuco forest in the LEF (Scatena *et al.* 1993) to estimate AGB of trees based on dbh. For taxa for which a species-specific equation was unavailable, we used a general allometric equation to estimate AGB (Scatena *et al.* 1993):

$$\mathrm{AGB} = e^{[2.475\ln(\mathrm{dbh})-2.399]} \tag{1}$$

where AGB is aboveground biomass of a particular tree in kg dry weight. Total AGB of a plot was calculated as the sum of the biomasses of all trees > 24.2 cm dbh in that plot.

BIODIVERSITY.—For each plot within each site, we calculated five measures of biodiversity: species richness, Simpson's diversity, Simpson's evenness, rarity, and dominance. Species richness (S) is the number of species in a plot. Simpson's diversity index (D) is calculated as

$$D = \frac{1}{\sum_{i=1}^{S} p_i^2} \tag{2}$$

where p_i is the proportional importance of species i (Magurran 1988). Simpson's evenness (E) was calculated as

$$E = \frac{D}{S} \tag{3}$$

where D is Simpson's diversity (Equation 2) and S is species richness (Smith & Wilson 1996). Rarity was defined as the proportion of rare species in a plot, where a rare species is one whose proportional importance is less than the average proportional importance of all species in that plot (Camargo 1993). Finally, dominance (d) is the maximum proportional importance (*i.e.*, the maximum p_i) of species in a plot (Berger & Parker 1970). Each index of biodiversity that involves weighting by p_i was calculated in two ways, once basing p_i on relative abundances and once basing p_i on relative biomass.

STATISTICAL ANALYSES.—For each site, we examined the relationship between each measure of biodiversity, including variants weighted by proportional abundance and proportional biomass, and AGB using regression analysis. The regression model for each dependent variable included a linear and quadratic component of AGB. We used Type III sums of squares so that priority was not assigned to linear or quadratic components in any regression model (Hays 1994). Because linear and quadratic components often are correlated highly in polynomial regressions, we centered AGB around its grand mean (the mean of the total AGB/m^2/plot) before conducting analyses, thereby avoiding multicollinearity (Neter *et al.* 1996, Chalcraft *et al.* 2009). We considered a relationship to be quadratic if it had a significant quadratic coefficient, indicating that the slope estimate of the quadratic term was significantly different from zero. To determine the amount of variability (R^2) in the dependent variable explained by the linear or quadratic components of AGB, we divided the Type III sums of squares for the linear (or quadratic) term in the regression model by the total sums of squares for the overall model. This procedure identifies whether linear or quadratic components independently explain a greater amount of variability in the dependent variable.

For regressions with a significant quadratic coefficient, we executed the Mitchell-Olds and Shaw (1987) test to determine if the relationship was unimodal or saturating. This test evaluates whether the vertex of the curve (*i.e.*, maximum biodiversity of unimodal or minimum biodiversity of U-shaped relationships) occurs at a value higher than the minimum AGB and lower than the maximum AGB in the data, respectively. If so, the relationship is unimodal or U-shaped. If not, the relationship is nonlinear but monotonic (see Mittelbach *et al.* 2001, Cox *et al.* 2006).

We tested whether the amount of variation associated with AGB (R^2) differed among sites using separate analyses of variance (ANOVAs) for each component of biodiversity. Within each site, we evaluated if the amount of variation explained by AGB differed among components of biodiversity using ANOVA. ANOVAs were conducted separately for the two methods used to quantify importance (proportional biomass vs. proportional abundance). When significant differences were found among sites, or among measures of biodiversity within a site, we identified those differences by comparing all pairs of sites or measures of biodiversity based on Tukey adjustments (Seneta & Chen 2005). Finally, we used ANOVA to determine whether the amount of variation explained in biodiversity–AGB relationships differed between indices based on proportional biomass vs. proportional abundance.

RESULTS

SHAPE OF THE RELATIONSHIPS.—Species richness evinced a unimodal relationship with AGB, except at Sabana 4, where the relationship was positive and linear (Table S1; Fig. 1). When weighted by proportional biomass, the shapes of the other biodiversity–AGB relationships differed widely among sites (Table S1; Figs. 2–5). When weighted by proportional abundance, the relationships were more consistent among sites (Table S1; Figs. 2–5). Regardless of the metric of biodiversity, biodiversity–AGB relationships at Sabana 4 differed from those at other sites (Table S1; Fig. 2–5). The relationship between Simpson's diversity and AGB was unimodal, except at Sabana 4, where it was nonsignificant (Table S1; Fig. 2). Rarity–AGB relationships were generally positive and linear, except at Sabana 4, where it was saturating (Table S1; Fig. 4). The shapes of relationships for other measures of biodiversity differed widely depending on site. Weighting by proportional biomass vs. proportional abundance had a profound effect on relationships (Table S1; Fig. 2–5). For unimodal relationships, the vertex occurred at standing stock values between 10.8 and 17.3 kg/m^2, except at Sabana 4, where it occurred at 22.2 kg/m^2 (Figs. 1–5).

STRENGTH OF THE RELATIONSHIPS.—Slightly more than half of the 36 relationships (four sites × four biodiversity measures × two weighting factors, plus the richness–AGB relationship for each of the four sites) had an R^2 value ≥ 0.15. The linear components of regression models usually accounted for more variation in the biodiversity–AGB relationships than did quadratic components, regardless of weighting factor. Thus, more of the variation in the relationships approximated a linear than a nonlinear relationship but a significant nonlinear component was present that accounted for some of the variation in the biodiversity–AGB relationships.

The amount of variation in biodiversity related to variation in AGB did not differ among sites when importance was estimated by proportional biomass ($F_{3,16} = 0.230$, $P = 0.874$) or proportional

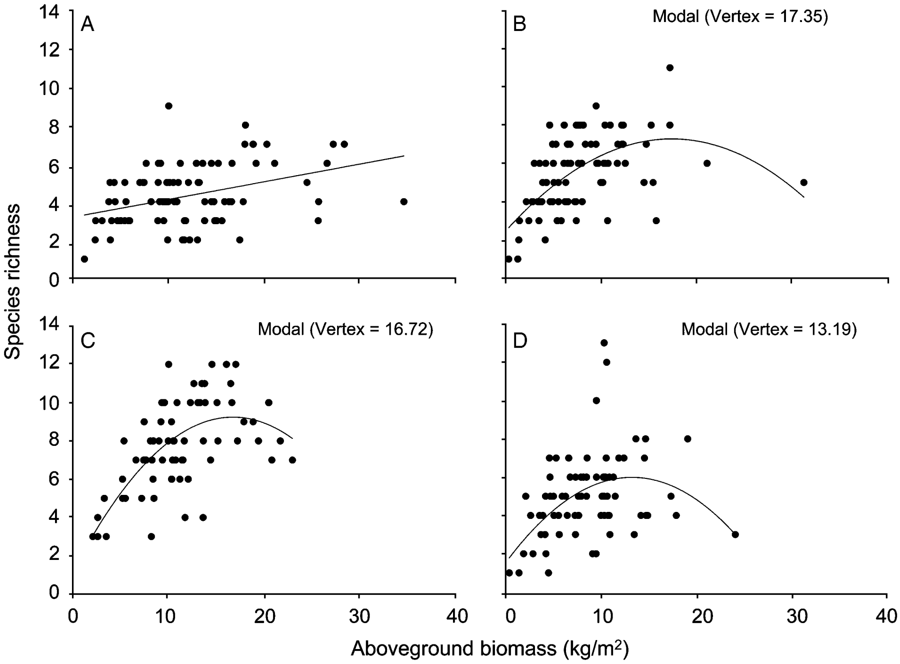

FIG. 1. The relationship between species richness and aboveground biomass (kg/m^2) at each of four sites in the Luquillo Experimental Forest: (A) Sabana 4, (B) Sabana 8, (C) Río Grande, and (D) Cubuy. If a relationship is significant, the appropriate regression line is plotted, with modal and monotonic relationships distinguished via the Mitchell-Olds and Shaw test.

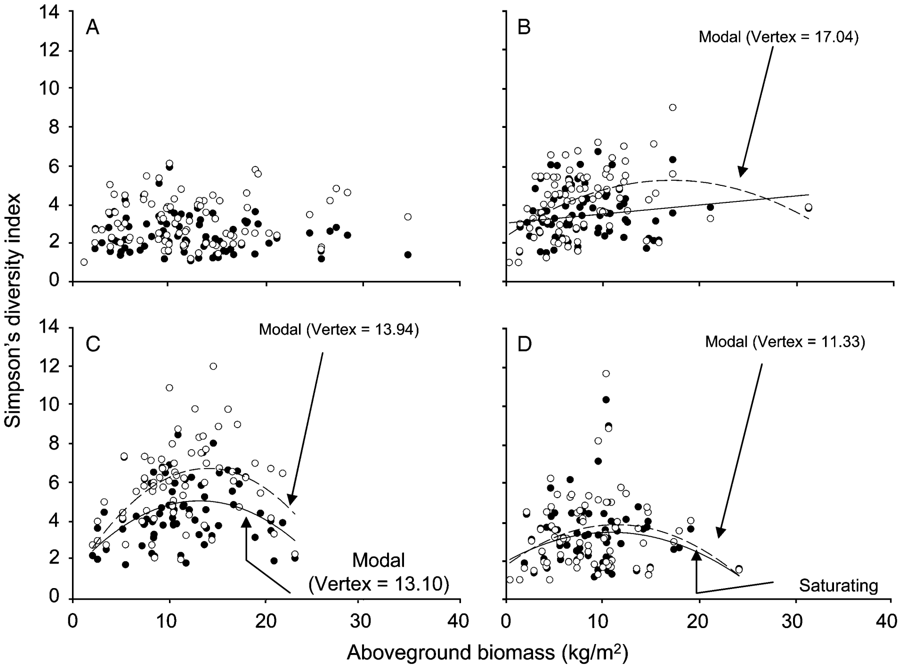

FIG. 2. The relationship between Simpson's diversity and aboveground biomass (kg/m^2) at each of four sites in the Luquillo Experimental Forest: (A) Sabana 4, (B) Sabana 8, (C) Río Grande, and (D) Cubuy. If a relationship is significant, the appropriate regression line is plotted, with modal and monotonic relationships distinguished via the Mitchell-Olds and Shaw test. Full circle and solid line indicate weighted by biomass, and empty circle and broken line indicate weighted by abundance.

abundance ($F_{3,16}=0.631$, $P=0.61$). However, the amount of variation explained by AGB was significantly different among measures of biodiversity when weighted by proportional biomass ($F_{4,15}=8.23$, $P=0.001$) or by proportional abundance ($F_{4,15}=4.29$, $P=0.016$). AGB accounted for significantly more of the variation in species richness and evenness (*ca* 1/3 of the variation) than in Simpson's diversity

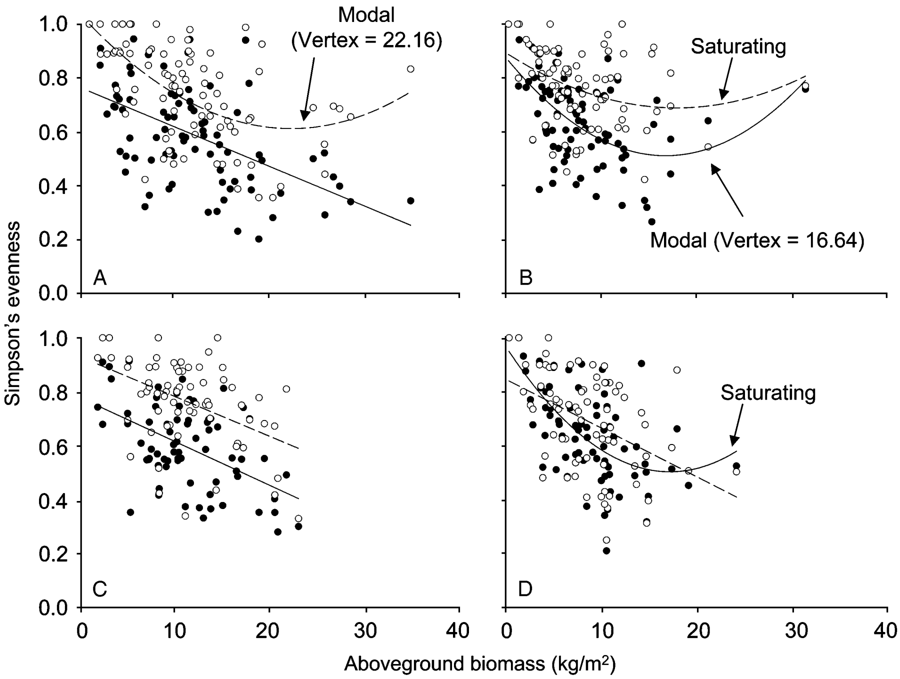

FIG. 3. The relationship between Simpson's evenness and aboveground biomass (kg/m^2) at each of four sites in the Luquillo Experimental Forest: (A) Sabana 4, (B) Sabana 8, (C) Río Grande, and (D) Cubuy. If a relationship is significant, the appropriate regression line is plotted, with modal and monotonic relationships distinguished via the Mitchell-Olds and Shaw test. Full circle and solid line indicate weighted by biomass, and empty circle and broken line indicate weighted by abundance.

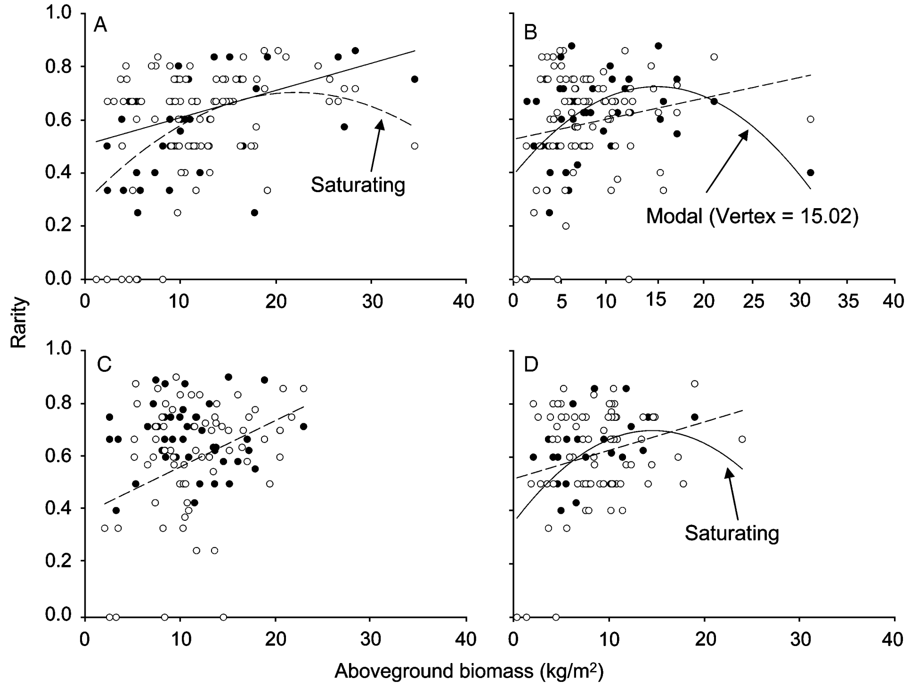

FIG. 4. The relationship between rarity and aboveground biomass (kg/m^2) at each of four sites in the Luquillo Experimental Forest: (A) Sabana 4, (B) Sabana 8, (C) Río Grande, and (D) Cubuy. If a relationship is significant, the appropriate regression line is plotted, with modal and monotonic relationships distinguished via the Mitchell-Olds and Shaw test. Full circle and solid line indicate weighted by biomass, and empty circle and broken line indicate weighted by abundance.

or dominance (all Tukey adjusted $P < 0.050$), when diversity indices were weighted by proportional biomass. AGB explained more of the variation in species richness than in dominance when the diversity indices were weighted by proportional abundance. Finally, the amount of variation in biodiversity that was associated with AGB did not differ between the weighting factors ($F_{1,30} = 0.328$, $P = 0.57$).

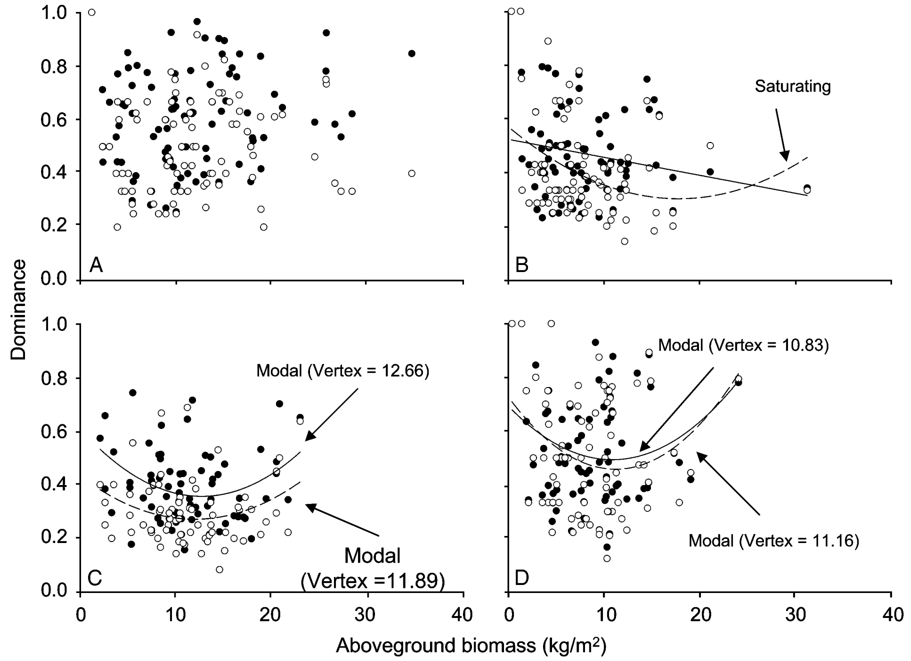

FIG. 5. The relationship between dominance and aboveground biomass (kg/m^2) at each of four sites in the Luquillo Experimental Forest: (A) Sabana 4, (B) Sabana 8, (C) Río Grande, and (D) Cubuy. If a relationship is significant, the appropriate regression line is plotted, with modal and monotonic relationships distinguished via the Mitchell-Olds and Shaw test. Full circle and solid line indicate weighted by biomass, and empty circle and broken line indicate weighted by abundance.

DISCUSSION

We have documented unimodal relationships between tree species richness and AGB in the secondary forest sites of a subtropical forest. Unimodal richness–AGB patterns are common in herbaceous grasslands, but not forests (Mittelbach *et al.* 2001). Community development patterns in response to disturbances may create the unimodal relationships we found between tree species richness and AGB at the secondary forest sites of the LEF. Major disturbances that affect the canopy of the LEF are tropical storms and hurricanes (Scatena *et al.* 1993, Zimmerman *et al.* 1994, Scatena *et al.* 1996). A 30-yr study of recovery from hurricane disturbance (Crow 1980) identified two distinct phases of community development in the LEF. During the first phase, tree stem density increased, along with stand biomass and species richness. During the later stage, stem density, species richness, and evenness decreased while stand biomass continued to increase, but at a much slower rate than during the first phase. The decrease in species richness as biomass continues to slowly increase may be due to competition for light, resulting in a few dominant species excluding other species (Keddy 2005, Healy *et al.* 2008). The idea that some tree species will be competitively excluded as biomass increases is supported by the evenness–AGB and rarity–AGB relationships. The negative evenness–AGB relationships suggest that a few species become more dominant at high biomass, instead of the biomass being distributed evenly among all species. Furthermore, the number of rare species increases as biomass increases, as indicated by the positive rarity–AGB relationships.

Sabana 4 is different from other sites in the LEF because it does not have a unimodal richness–AGB relationship, and has the fewest significant relationships (Table S1). Such differences may be related to prior land use and successional state, as Sabana 4 is the only mature forest site. Although Sabana 4 experiences hurricane damage similar to the other sites, it became mature forest because it was never cultivated or used as pasture. As succession proceeds in forests, many changes in species richness and AGB occur. Results for Sabana 4 suggest that as succession progresses, the strength of the relationship between multiple measures of diversity and AGB weakens. Thus, the community development phases documented by Crow (1980) may only reflect hurricane recovery in secondary forest. Other local site conditions may be more important in determining species diversity in mature sites (see Scatena & Lugo 1995). For example, soil quality, drainage, and topography can strongly influence relationships between species richness and biomass production (Healy *et al.* 2008).

The vertex of unimodal relationships in the LEF (*i.e.*, maximum species richness, Simpson's diversity index, and rarity, as well as minimum evenness and dominance) occur approximately at the mid-point of the observed AGB values for each site. These intermediate values of AGB are smaller than the average AGB at mature forest stands in the LEF (*e.g.*, Bisley, El Verde, ridge stands). This result is not surprising, however, since our sites (with the exception of Sabana 4) are secondary forest sites instead of mature forest stands. Although Sabana 4 is a mature site, the smaller than average values of AGB in our study at this site may be explained by the influence of a prior hurricane. Hurricane Hugo crossed the LEF in September 1989, 2 yr before data collection, bringing high wind velocities and higher than usual rainfall amounts (Scatena & Larsen 1991; Scatena *et al.* 1993, 1996; Parresol & Alemañy 1998). Aboveground live biomass likely was lower during our data collection than it was before the storm since some woody biomass blew to the forest floor during the storm. In addition, our analyses pertain to large trees (dbh > 24.2 cm); we do not include young pioneer tree species that colonized after the storm due to limitations of the data set.

Either the frequency and scale of the disturbances (Chesson *et al.* 2002) experienced in the LEF or the spatial scale of analysis, or a combination of both, may explain why richness–AGB relationships were unimodal whereas other forest studies have not detected such patterns (Wardle *et al.* 1997, Caspersen & Pacala 2001, Vila *et al.* 2003, Erskine *et al.* 2006, Sagar & Singh 2006, Houle 2007, Vila *et al.* 2007). First, disturbance regimes differ greatly among tropical areas and may account for critical differences in species richness–AGB relationships (Phillips *et al.* 1994). Compared with the LEF, many tropical forests experience more frequent or smaller-scale disturbances (Phillips *et al.* 1994). For example, dry forests in India experience frequent, large-scale human disturbances from mining, power generation, cattle ranching, and extraction of forest resources (Sagar & Singh 2006). In these forests, a positive linear relationship exists between biodiversity and total tree basal area (a surrogate for biomass), perhaps because continual disturbance does not allow biomass to concentrate in only the strongest competitors (Sagar & Singh 2006). In contrast, the main disturbances (*e.g.*, hurricanes) in the LEF are infrequent and long recovery periods are typically available (*e.g.*, the 30-yr recovery period studied by Crow 1980) in which biomass can accrue and competition for light may become important. Second, aspects of spatial scale (focus and extent) differ among studies, and the richness–AGB relationship is scale-dependent (Keddy 2005). We found a unimodal richness–AGB pattern within a community type along a short spatial extent (*i.e.*, within the LEF) whereas Caspersen and Pacala (2001) found a positive relationship when comparing forest sites across a large spatial extent (11 Midwestern states in the United States).

Evenness–AGB relationships are as strong as richness–AGB relationships within sites, but of opposite shapes. For example, richness has either a unimodal or positive linear relationship with AGB, whereas evenness has a negative linear or positive monotonic relationship with AGB. Consequently, studies of community structure should consider both richness and evenness because they represent different aspects of biodiversity and because they have different relationships with AGB.

Part of the variation (12–43%; Table S1) in richness and evenness in the LEF is related to the amount of AGB. Local environmental factors, such as soil fertility, topography, and elevation, likely explain the remaining variation in richness and evenness. The relationship between Simpson's diversity, rarity, or dominance with AGB was weaker generally than richness or evenness relationships with AGB. Thus, abiotic conditions or other factors are more important than AGB in determining biodiversity in these plots.

The identity of the weighting factor (*i.e.*, proportional biomass vs. abundance) influences the form of biodiversity–AGB relationships, but in subtle ways. For example, the shape of the relationship between evenness and AGB, as well as between rarity and AGB, was more variable among sites when biomass was used as the weighting factor than when abundance was used. This difference may indicate that the four sites differed in the identity of the rare species present. The tree species with low abundance in some sites may have been species with relatively low biomass whereas the tree species that had low abundance in other sites may have much higher biomass. In this latter case, weighting by abundance would count these uncommon species as rare, but weighting by biomass would not consider these species to be as rare. A *post-hoc* comparison found marginal support for this idea, with a marginal difference ($P = 0.09$) among sites in the average biomass per m^2 of the species that had an abundance of three or fewer individuals per site.

In tabonuco forest, weighting by proportional abundance is the more accurate and precise measure since we could determine tree abundance directly but could only estimate biomass using allometric equations based on dbh. Despite the subtle effects we documented based on the identity of the weighting factor, comparisons between studies that weight measures of biodiversity by proportional biomass and those that weight by proportional abundance should be made with a great deal of caution.

This paper contributes new information to our understanding of biodiversity–AGB relationships in subtropical forests, suggests mechanisms to explain these patterns, and discusses the often overlooked consequences of weighting richness by relative biomass vs. relative abundance. However, the limitations of our data set leave several unanswered questions. For example, would the biodiversity–AGB relationships we documented change if data on post-hurricane growth (in the form of small trees) had been available for these plots? What is the influence of plot size on our results? And, what relationship exists between tree functional characteristics and AGB? Interest in the role of functional similarity on biomass production, in particular, is evident in several recent studies (Hooper *et al.* 2005, Spehn *et al.* 2005, Jiang *et al.* 2007, Maherali & Klironomos 2007, Szwagrzyk & Gazda 2007, Vila *et al.* 2007). In many cases, functional group richness seems to be as related as species richness to AGB.

In summary, unimodal species richness–AGB relationships are prevalent in subtropical forest sites in the LEF of Puerto Rico, except at the most mature site. The biodiversity–AGB patterns have been influenced by prior land use and infrequent, large-scale disturbances (*i.e.*, hurricanes). These storms may help maintain higher levels of biodiversity by reducing the accumulation of aboveground live biomass and preventing one or a few species from excluding less common or competitively inferior species.

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SUPPORTING INFORMATION

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

TABLE S1. *Results (R^2) of Type III sums of squares polynomial regression analyses to assess the form and parameterization of the relationship between each of a number of measures of biodiversity and aboveground biomass.*

APPENDIX S1. Limitations of methodology.

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